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THE EFFECT OF TEMPERATURE AND MOISTURE ON THE IMMATURE STAGES OF *APHODIUS TASMANIAE* HOPE (SCARABAEIDAE) IN THE LOWER SOUTH-EAST OF SOUTH AUSTRALIA*

By D. A. MAELZER†

[*Manuscript received November* 14, 1960]

Summary

The distribution and abundance of the univoltine species *A. tasmaniae* in the lower south-east of South Australia appears to be related to annual rainfall. The effects of moisture on the mortality rates of the immature stages were consequently studied and observations were made of the effects of variations in moisture in the field.

Laboratory experiments and field observations suggested that variations in soil moisture have little effect on the eggs and the diapausing prepupae in the field. Eggs absorbed water and hatched normally within a pF range of 2·50–3·75 in a sand and in a clay loam. At pF 4·0 in both soils, eggs lost weight and did not hatch. The adults, however, tend to lay the eggs well within the pF range in which the eggs can develop, and soil samples suggested that eggs would develop with little mortality in the kinds of places in which they are usually laid.

When prepupae enter diapause they have a water content of *c.* 77%. When desiccated in the laboratory, few prepupae died until their water content fell below 62%. The mortality rate then increased sharply, and it was estimated that 50% of the prepupae died when their water content dropped to 57%. Droughts of sufficient duration and intensity to kill 50% of the prepupae have never been recorded from the study area, and field observations suggested that few prepupae died of desiccation in summer.

Unlike the two stages above, the first and third instar larvae may be markedly affected by variations in moisture in the field. The first instar larvae, after hatching, do not move to the surface of the soil and do not feed much until the soil is saturated with rain. As rainfall is variable at this time of the year, the larvae may be in dry soil for many weeks before they are stimulated to extend their burrows to the surface and search for food. Many larvae may die of starvation during this time, and the mortality rate of the larvae was related empirically to the length of the autumn "drought".

Third instar larvae may be affected, on the other hand, by excessive water. In wet winters, vast numbers of larvae are drowned when extensive flooding occurs on the poorly-drained soils, and on well-drained soils a large proportion of larvae are killed by the entomophagous fungus *Cordyceps aphodii*.

The above data have suggested that moisture is one of the major factors affecting the distribution and abundance of the species.

Temperature has little effect on the rate of increase of the species.

* Part of a thesis accepted by the University of Adelaide for the Ph.D. degree.

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I. Introduction

Aphodius tasmaniae Hope has been an economic pest of improved pastures in southern Australia for about 30 years (Carne 1956). The species is widely distributed in South Australia but is particularly prominent as a pasture pest in the

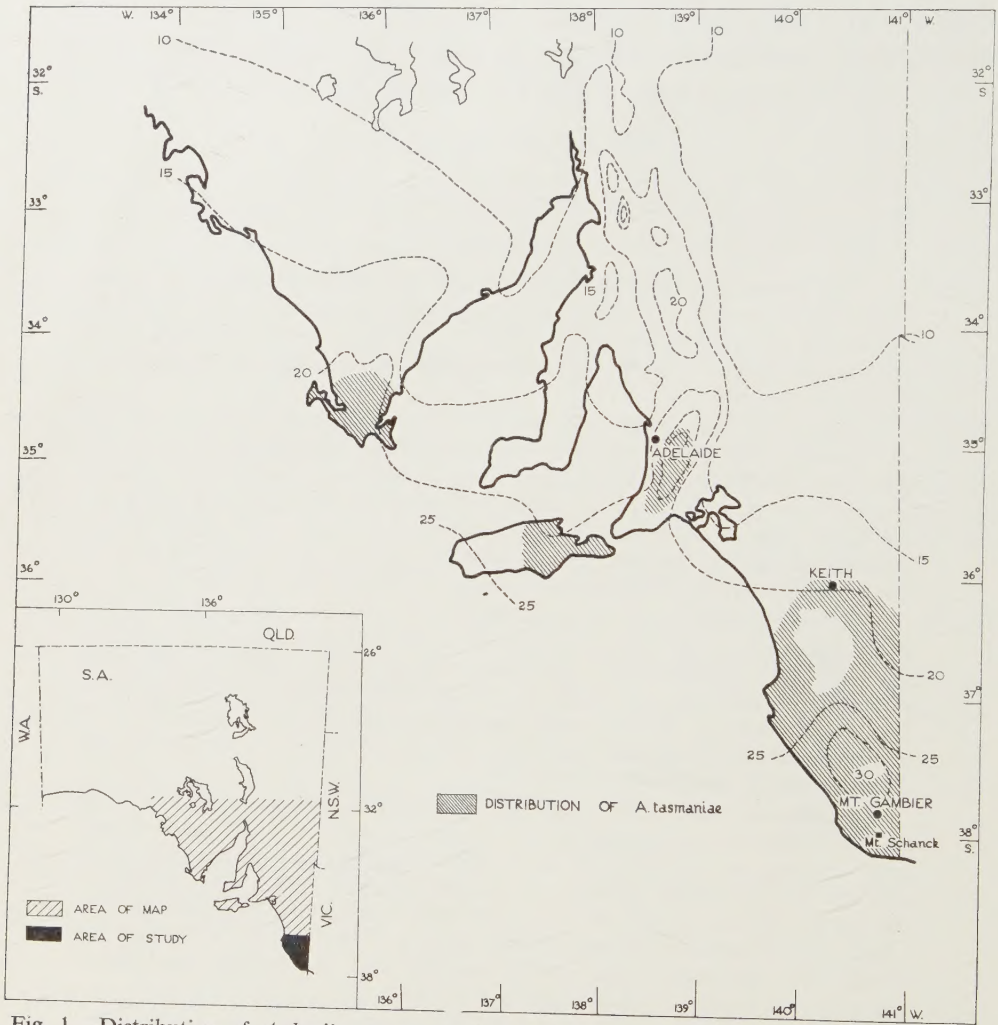

Fig. 1.—Distribution of *Aphodius tasmaniae* in South Australia in relation to annual rainfall (after Madge 1952). Isohyets in inches.

lower south-east, which is the largest area in the State with an assured rainfall (Fig. 1). The distribution of the species in the State in relation to rainfall (Fig. 1) suggested that moisture was one of the major factors influencing this distribution, and preliminary work on the species in the lower south-east suggested that moisture was indeed one of the major factors influencing the rate of increase of the species (Swan 1934; Andrewartha 1945; Madge 1952). Moisture is often

deficient in summer and in excess in winter (Table 1). In summer the mortality rate of the eggs and young larvae may be affected by desiccation and in winter the older larvae may be drowned or killed by the fungus *Cordyceps aphodii* Mathieson. The same authors also suggested that temperature affected the rate of development of the immature stages but had little or no resultant influence on the rate of increase of the species because the species is univoltine. Mean monthly air and soil temperatures for the lower south-east are given in Table 1. The data are from Mt. Burr, about 30 miles from Mt. Gambier.

TABLE 1

MEAN MONTHLY RAINFALL AND ESTIMATED MEAN EVAPORATION FOR MT. GAMBIER (AFTER TRUMBLE 1948), AND AVERAGE DAILY MEAN SOIL AND AIR TEMPERATURES FOR TWO LOCALITIES IN THE LOWER SOUTH-EAST OF SOUTH AUSTRALIA

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Rainfall (in.)*	1·34	1·03	1·42	2·38	3·33	3·91	4·04	3·86	3·09	2·40	1·72	1·62
Evaporation (in.)	6·5	5·2	4·0	2·5	1·4	1·1	1·1	1·4	2·3	3·6	4·4	5·6
Soil temperature (°C), Mt. Burr†	19·4	19·2	18·0	15·1	12·5	10·3	9·2	9·4	11·1	13·2	15·4	17·9
Air temperature (°C), Mt. Burr‡	17·1	17·1	16·2	13·5	11·3	9·4	8·9	9·4	10·9	12·1	13·8	16·5
Air temperature (°C), Mt. Gambier§	18·0	18·5	17·0	14·4	12·1	10·3	9·5	10·3	11·6	13·3	14·9	16·6

* Means for 82 years; mean total 30·14 in.

† At depth of 6 in.; means for 18 years.

‡ Means for 11 years.

§ Means for 30 years.

This paper deals with the effect of moisture on the mortality rate of the immature stages of *A. tasmaniae*, and with the effect of temperature on the rate of development of eggs and on the rate of completion of diapause development of the over-summering prepupa. It is the second of a series of papers on the ecology of *A. tasmaniae* in the lower south-east of South Australia. The first paper (Maelzer 1961) includes a study of the effect of moisture on the adult.

II. The Effect of Temperature

It was confirmed during this study that the immature stages of *A. tasmaniae* are rarely, if ever, exposed to lethal temperatures in the lower south-east of South Australia, and that variations in temperature in this area have little effect on the longevity of the species in the field and hence little effect on its rate of increase.

The following two aspects of the effect of temperature on the rate of development of the immature stages were, however, of interest for reasons given below.

(*a*) *Rate of Development of Eggs at Constant Temperature*

The eggs of *A. tasmaniae* hatch at a time of the year when moisture may be deficient and may influence markedly the mortality rate of the young larvae. To estimate the effect of moisture on the mortality rate of larvae in the past it was necessary to estimate when eggs hatched. The rate of development of eggs at constant temperatures was therefore determined.

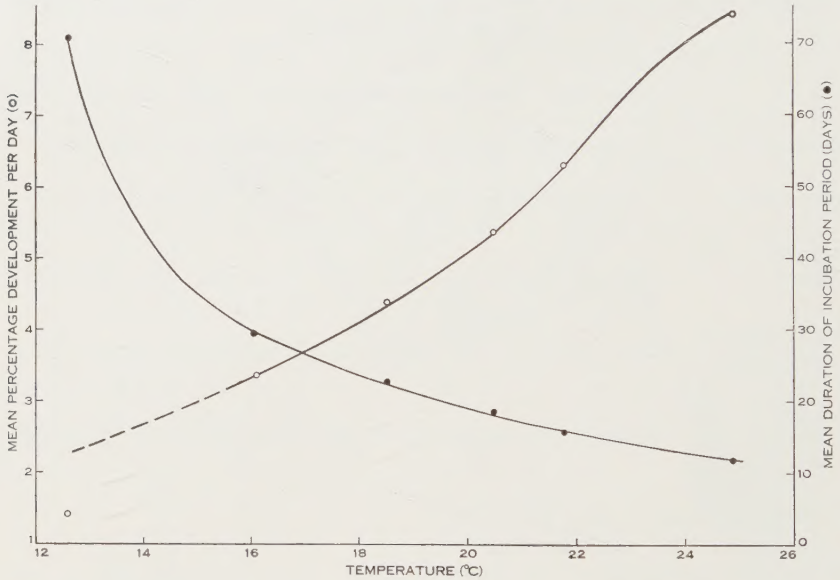

Fig. 2.—Development of eggs of *A. tasmaniae* at constant temperatures.

Eggs which were 0–24 hr old were placed on moist filter paper in petri dishes at various constant temperatures and the numbers of larvae which hatched each day were recorded. The mean duration of the incubation period was then calculated for each temperature.

Davidson (1944) used the logistic curve to express the relationship between temperature and the rate of development of insects, but Browning (1952) showed that, although this curve closely followed the observed points, deviations of the points from the curve were significant. The mean duration of the incubation period was, therefore, plotted against temperature and a free-hand curve was drawn through the observed points (Fig. 2). The mean percentage development per day was likewise calculated and a free-hand curve drawn through the points. These computations were considered adequate for ecological purposes.

(*b*) *Effect of Temperature on Diapause Development*

The larvae of *A. tasmaniae* stop feeding about the end of September each year, discard their gut contents, and construct cells in the soil in which they live for 3–4 months. They have by this time accumulated much fat which gives them a creamy yellow appearance and are morphologically prepupae (Lower 1957). When prepupae were kept in moist soil over the early months of summer they did not pupate any earlier than they did in the field, so it was concluded that the prepupae did not simply suspend development because of a lack of water in the soil but entered an obligate diapause.

TABLE 2

EFFECT OF TEMPERATURE ON DIAPAUSE DEVELOPMENT

Pupation of diapausing prepupae after 13 weeks at different temperatures

Temp. (°C)	No. of Insects Alive (out of 50)	No. of Pupae	Pupae (%)
13·5	31	0	0
15·8	23	1	5
18·0	20	11	55
20·3	24	22	91
24·8	18	14	78
26·0	17	8	48
13·5 (10 days)*	24	20	83
13·5 (20 days)*	18	11	61
13·5 (30 days)*	16	8	50
13·5 (40 days)*	17	1	6

* Insects at 13·5°C for 10, 20, 30, and 40 days, respectively, and then at 18·0°C.

Prepupae were collected in the first week of October and were placed in tubes of moist soil. They were then randomized into 10 groups, of which six were placed at 13·5, 15·8, 18, 20·3, 21·8, and 26°C; the other four groups were kept at 13·5°C for 10, 20, 30, and 40 days, respectively, and then transferred to 18°C. The main treatment temperatures (13·5 and 18°C) were chosen to approximate to the mean monthly soil temperatures at a depth of 6 in. at Mt. Burr for October and December (Table 1).

The numbers of pupae at the different treatments were recorded 13 weeks after the start of the experiment and shortly after the insects had started to pupate in the field. The results are given in Table 2. Fifty larvae were used in each treatment, but fungal infections drastically reduced the numbers of survivors. The results are consequently based on small numbers, but the following trends may be noticed:

(1) Morphogenesis did not proceed or proceeded very slowly at 13·5°C.

(2) Prepupae which had been kept at 13·5°C for 10 days and then transferred to 18°C developed more rapidly than those which had been kept at 18°C continuously, whilst prepupae which had first been at 13·5°C for 20 and 30 days developed about as rapidly as those kept continuously at 18°C. Diapause development thus proceeded more rapidly at 13·5°C than at 18°C.

(3) The continuous temperature at which diapause development *plus* morphogenesis proceeded most rapidly was 20·3°C. At higher temperatures the percentage pupation decreased, and it is tempting to suggest that morphogenesis should proceed more rapidly at temperatures above 20·3°C and that, therefore, diapause development proceeded more slowly at temperatures higher than 20·3°C. However, the mean monthly temperature for January (when the insects pupate in the field) in the lower south-east is about 20°C, so it is likely that morphogenesis does, indeed, occur most rapidly at this temperature.

(4) Although the percentage pupation decreased at temperatures above 20·3°C, it was high, even at 26°C.

Since diapause development at 13·5°C is more rapid than at 18°C it is likely that it is also more rapid than at 20·3°C. If this is so, diapause development in *A. tasmaniae* would be similar to that of many other insects in that it would proceed most rapidly around the lowest temperature favourable for morphogenesis (Andrewartha 1952). Diapause development in *A. tasmaniae* seems, however, to be somewhat atypical in that considerable diapause development seems to be possible over much of the range of temperature favourable for morphogenesis.

III. Effect of Moisture

(*a*) *Effect of Moisture in Soil on the Absorption of Water by Eggs and on their Viability*

The eggs of *A. tasmaniae* are found in batches in the soil at a depth of about 6 in. They need contact water for development, like the eggs of many other insects which are laid in soil. They are laid, however, in late summer when lack of moisture is probably the major hazard limiting their chance of survival. Some information was therefore required of the ability of eggs to absorb water from soil.

There are numerous ways of measuring water in soil but it has been shown (Evans 1944; Evans and McGuild 1948; Maelzer 1961) that it may be useful when considering the effect of moisture on animals in different soils to measure moisture in terms of the force with which water is held, i.e. the pF scale — or some equivalent scale of hydrostatic pressure — rather than in terms of water content. The following experiment was therefore conducted to determine whether soil pF was a better measure of the ability of eggs of *A. tasmaniae* to absorb water from the soil than its water content, and of their mortality rate in two soils.

(i) *Method.*—The experiment was conducted at 20·2°C, at which temperature eggs (1) start absorbing water on the 5th-6th day; (2) absorb water most rapidly

on about the 10th day; (3) absorb little water after about the 14th day; and (4) start to hatch on about the 16th day.

The experiment was conducted with two soils, a clay loam and a sand, which were used in previous experiments (Maelzer 1961). There were 13 treatments altogether, two soils each at six pF values and one of moist filter paper over water. The soils were moistened and allowed to dry slowly to the required water contents; since the pF curves derived for the two soils were drying curves, the soil–water energy relations in this experiment were consequently more closely defined than in the previous experiments (Maelzer 1961).

TABLE 3

MEAN CHANGES IN WEIGHT OF EGGS OF A. TASMANIAE IN RELATION TO MOISTURE IN TWO SOILS

All changes in weight (in mg/mg original wt.) positive except those with negative signs. Mean weight of an egg before the experiment was 0·478 mg

Type of Soil	pF of Soil						Eggs on Moist Paper*	Mean for Soils
	2·50	3·00	3·25	3·50	3·75	4·00*		
Sand	1·669	1·596	1·542	1·395	1·022	−0·338	1·522	1·444
Clay loam	1·622	1·554	1·579	1·537	1·069	−0·258		1·458
Mean	1·646	1·575	1·560	1·466	1·045	−0·298		1·451

Analysis of Means of pF Values 2·50–3·75

Comparing Means	S.E. of Difference	Difference for Significance at $P =$		
		0·05	0·01	0·001
Any two pF values	0·0835	0·179	0·249	0·346

* Not included in totals, means, and the analysis of variance.

Quantities of soil of the required water contents were placed in bottles with airtight lids and stored at 20·2°C for 2 weeks, during which time they were shaken 5–6 times a day. Eggs were then placed in plastic tubes filled with soils of the required water contents. Weighing of the tubes of soil after the experiment showed that a negligible amount of water had been lost.

The eggs were obtained when they were 0–24 hr old and were allotted singly and at random within three replicates. There were 10 eggs in two groups of five in replicates 1 and 2, and 17 eggs in replicate 3. The eggs in replicates 1 and 2 were weighed in groups of five on the 5th day when water absorption was expected to commence. About half the eggs did not absorb water during the course of the experiment; at pF values at which other eggs *did* absorb water, the eggs which did not absorb water were considered sterile and were rejected when

estimating water absorption. The survivors of each group of five were then weighed in their groups on the 15th day after being washed in solutions of sodium chloride, the osmotic pressures of which were equivalent to the suction forces in the soils of the different treatments. The numbers of eggs which hatched were recorded later.

(ii) *Results.*—There was no significant difference between the original mean weights of eggs ($F < 1{\cdot}0$ with 12 and 51 d.f.; $P > 0{\cdot}2$) so the original mean weights were used to calculate mean changes in weight of eggs after treatment. These changes in weight are given in Table 3 in terms of the mean change in weight of eggs in milligrams per milligram of original weight.

The null hypothesis was that there would be no significant differences in the amounts of water absorbed by eggs at the same pF values in the two soils.

All the eggs at pF 4·0, unlike the eggs at other pF values, appeared crinkled and had lost weight in both soils, whereas some of the eggs at all other pF values gained weight. The eggs at pF 4·0 were so obviously different from the others that the mean losses in weight of eggs in the two soils at this pF value were compared separately and found not to be significantly different ($t = 2{\cdot}34$, $P > 0{\cdot}05$). The mean increases in weight of eggs at the other pF values were subjected to an analysis of variance; no significant difference was found between soils ($F < 1{\cdot}0$ with 4 and 30 d.f.; $P > 0{\cdot}2$). The data suggest, therefore, that the absorption of water by eggs in the two soils was related to the pF value of the soil.

The analysis of variance also indicated that the differences in the mean increases in weight of eggs at pF values 2·50–3·75 could not be attributed to chance ($F = 16{\cdot}46$ with 4 and 30 d.f.; $P < 0{\cdot}001$). The differences required for significance (Table 3) indicated that eggs at pF 3·75 absorbed less water than eggs at pF 3·50 ($P < 0{\cdot}001$). Similarly eggs at pF 3·75 absorbed less water than eggs on moist paper ($t = 5{\cdot}51$, $P < 0{\cdot}001$) but the differences in water uptake on moist paper and at pF values 2·50–3·50 were not significantly different (largest $t < 1{\cdot}0$; $P > 0{\cdot}2$).

The percentage emergence of larvae from eggs at the different treatments after 25 days is given in Table 4. The emergence was low in all treatments apparently because about half the eggs were sterile. Nevertheless the null hypothesis, i.e. that there were no significant differences in emergence between the same pF values in the two soils, was tested.

The eggs which had lost weight in soil at pF 4·0 were placed on moist filter paper for a few days but they did not develop and were considered to have died or to have been sterile. The mortalities of eggs in soil at this pF value were so obviously different from those in all other treatments that they were omitted from the subsequent statistical analysis. The percentage emergences at the other pF values were transformed to degrees and subjected to an analysis of variance. No significant difference was found between treatments (soils × pF values) ($F = 1{\cdot}47$ with 10 and 22 d.f.; $P > 0{\cdot}2$; see Table 4). This finding, coupled with the total lack of survivors in both soils at the pF value 4·0, suggests that the mortality rate of the eggs of *A. tasmaniae* was a function of the energy with which water was held in the two soils.

Although eggs absorbed more water at pF 3·50 than at pF 3·75 there was no significant difference in the percentage emergence of larvae from eggs at these pF values. The mean incubation period, however, was not noted, and it is not known whether the eggs at pF 3·75 hatched without their full complement of water or whether development was slower and the eggs hatched later after having absorbed the same amount of water as those at lower pF values.

(*b*) *Tolerance of First Instar Larvae to "Drought" before Migration to the Surface of the Soil*

Laboratory observations suggested that the first instar larvae, after hatching, migrated to the surface of the soil only when the soil was wet; and it seems that in the field they migrate to the surface only after rain has penetrated the soil to the depth at which the eggs were laid. The occurrence of suitably heavy falls of

TABLE 4

PERCENTAGE EMERGENCE OF LARVAE FROM EGGS AT VARIOUS pF VALUES IN TWO SOILS

Replicate No.	Number Used in Replicate	Soil Type	Emergence (%) of Larvae in Soils at pF:						Emergence on Moist Paper (%)
			2·50	3·00	3·25	3·50	3·75	4·00	
1	17	Sand	29	41	53	47	41	0	59
2	10		40	50	30	20	30	0	50
3	10		50	70	60	40	30	0	50
1	17	Clay loam	47	47	41	53	59	0	
2	10		40	40	30	50	50	0	
3	10		60	50	50	60	40	0	

rain (the "break" of the season) varies considerably from year to year, and in some years larvae apparently do not migrate to the surface until 4–6 weeks after hatching. It had been suggested (Andrewartha 1945) that the lateness of the break of the season affected the mortality rate of larvae. Some measure was therefore necessary of the ability of larvae to tolerate drought before they migrated to the surface of the soil.

(i) *Effect of Drought on Larval Mortality Rate in the Field.*—The effect of a prolonged dry spell on the mortality of larvae can best be assessed in the field by "seeding" plots with adults and estimating the number of eggs laid and the percentage mortality of the young larvae at the termination of the dry spell. Such estimates were derived from two field experiments, one consisting of eight and the other of six plots, which had been primarily designed to determine where females aggregated and laid eggs (Maelzer 1961). Instead of sampling the plots for adults and eggs, the plots were left intact for 1–2 months and were sampled at appropriate intervals to estimate larval mortality.

The recording of dead adults as well as live larvae in the plots (Table 5) enabled estimates to be made of the number of live larvae per adult at any time. The proportions of larvae to adults recorded in the plots at any one time were roughly constant and lend confidence to the estimate of larval mortality which was based on the changing proportions of larvae to adults.

The females were placed on the plots on February 16, 1955. It was expected that they would have laid their eggs by February 19–20 and that 50% of the eggs would have hatched by March 13. The first plots were examined on March 22–24,

TABLE 5

EFFECT OF "DROUGHT" ON THE MORTALITY RATE OF LARVAE BEFORE MIGRATION TO THE SURFACE IN THE FIELD

Number of insects in plots dug up soon after all eggs had hatched and after an estimated 30 days of drought

After Hatching				After Drought			
Plot No.	Dead Adults	Larvae	Larvae per Adult	Plot No.	Dead Adults	Larvae	Larvae per Adult
1	62	757	12·2	1	11	49	4·1
2	38	548	14·4	2	70	262	3·7
3	63	720	11·4	3	53	157	3·0
4	14	159	11·4	4	51	270	5·3
				5	12	73	6·1
				6	124	731	5·9
				7	89	547	6·2
				8	4	13	3·3
				9	136	889	6·5
				10	95	602	6·3
Total	177	2184			645	3593	
Mean			12·34				5·57

and it was found that all but three of the eggs had hatched and the first instar larvae were all within the cells in which the eggs were laid. The proportions of larvae to adults in the four plots examined were 12·2, 14·4, 11·4, and 11·4 (Table 5) with a mean of 12·3.

Migration of the larvae to the surface of the soil in the other plots was inhibited by a lack of "effective" rain until more than an inch fell on April 12. Another lot of plots was dug up on April 22 after the larvae had migrated to the surface; the proportions of larvae to adults recorded had a mean of 5·6 (Table 5).

It is unlikely that many eggs or young larvae died between the time when they hatched and the time when the first plots were examined. The reduction in the number of larvae per adult observed between March 22 and April 22 thus roughly measures the percentage mortality of the first instar larvae from the

estimated time of hatching (March 13) to the time when the soil was wetted (April 12). It is, therefore, estimated that after the 30 days of autumn drought the number of larvae per adult dropped from 12·2 to 5·6, i.e. about half the larvae died.

(ii) *Effect of Drought on Larval Mortality Rate in the Laboratory.*—The following laboratory experiment was conducted to obtain a further estimate of the effect of drought on the mortality rate of the young larvae and to determine the cause of death of the larvae during drought.

A preliminary experiment indicated that the mortality rate of young larvae was a function of the time they spent in dry soil. It appeared that the larvae did not feed much in dry soil and remained in tiny, individual cells not far from where the eggs were laid until the soil was moistened. During a period of drought they could die either from starvation or from desiccation, so the experiment was designed to determine the effect of both these factors on their mortality rate. An initial experiment had also indicated that, in two soils, migration of larvae to the surface occurred at pF 2·50 but was inhibited in soil drier than pF 3·00. So larvae were kept in sand of pF values 3·30, 3·80, and 4·10 for 1, 2, 3, and 5 weeks. The required pF values were obtained by drying the sand after it had been moistened; the sand was then tamped down in wax paper cups.

Newly hatched larvae were randomized into groups of 10. Each group of 10 was then weighed and the larvae were placed in a cell near the bottom of a cup of soil. There were five groups (replicates) for each treatment. Food was placed on the surface of the soil so the larvae could feed as soon as they migrated to the surface and the cups of soil were covered with polythene sheeting and stored in an incubator at 18·0 ± 0·1°C. After the required period of time each cup was weighed to estimate the amount of water lost and hence its water content, and a record was made of the number of larvae alive and their weight as a group. The insects were then discarded.

Fifty larvae were also kept in sand at a pF value of 2·50. This group constituted the control, for it was expected that at this pF value the larvae would feed continuously, develop rapidly, and suffer little mortality. These larvae were examined after the same intervals of time as those in sand at the other pF values. Instead of being discarded they were, however, replaced after each examination; so the same insects constituted the control throughout the experiment. After each examination their food was renewed and the soil in which they lived was wetted to approximate to a pF value of 2·50.

The numbers of larvae alive after treatment are given in Table 6. The data for pF 2·50 were not included in the analysis of variance which was based on the numbers of larvae alive at pF values of 3·30, 3·80, and 4·10 transformed to $(x + \frac{1}{2})^{\frac{1}{2}}$ (Table 6). This analysis suggested that there were significant differences in the numbers of larvae alive at the different times ($F = 31{\cdot}55$ with 3 and 48 d.f.; $P < 0{\cdot}001$), but that the interaction of pF × time and the differences between pF values could be attributed to chance (both values of $F < 1{\cdot}5$). The differences required for significance are given in Table 6.

The mortality of larvae at pF 2·50 enables the analysis to be taken further. A χ^2 test indicated that the numbers of larvae in the treatments and at pF 2·50 after 1 week were not significantly different, but the differences in mortality between pF 2·50 and the treatments after 2, 3, and 5 weeks were all highly significant

TABLE 6

MEAN NUMBERS OF FIRST INSTAR LARVAE ALIVE (OUT OF 10) AFTER 1, 2, 3, AND 5 WEEKS IN SOIL AT FOUR pF VALUES

Time (weeks)	pF 2·50*		pF 3·30		pF 3·80		pF 4·10		Mean of Times (transformed values)
	Mean No. of larvae	Transformed Value†	Mean No. of Larvae	Transformed Value†	Mean No. of Larvae	Transformed Value†	Mean No. of Larvae	Transformed Value†	
1	7·6	2·742	6·8	2·690	7·4	2·770	7·8	2·874	2·778
2	7·6	2·742	5·0	2·308	5·2	2·372	4·4	2·198	2·293
3	7·6	2·742	3·4	1·954	2·0	1·500	4·8	2·280	1·911
5	7·4	2·708	1·2	1·196	0·8	1·118	1·6	1·314	1·209
Means		2·734		2·037		1·940		2·167	2·048

Analysis of Means

Comparing Means	S.E. of Difference of Means	Difference for Significance at $P =$		
		0·05	0·01	0·001
Any two times	0·1667	0·341	0·461	0·613
Any two pF values	0·1291	0·261	—	—

* Control, not included in the means of times and in the analysis of variance.

† Means of individual values transformed to $(x+\frac{1}{2})^{\frac{1}{2}}$.

($P < 0·01$). The mortality of larvae after 1 week could thus have been due to chance or experimental error, but the mortality of larvae in the treatments between 1 and 5 weeks could not be attributed to either of these sources of error.

The sand dried out more than expected during the course of the experiment, but the larvae *were* exposed to different levels of desiccation for at least 3 weeks (Table 7). Since there was no difference in mortality between pF values it is likely

therefore that the larvae died of starvation rather than water loss after the first week.

The mean increases in weight of the larvae are not at variance with the hypothesis that the larvae died of starvation. The differences in the weights of groups of larvae before the experiment were not significant ($F = 1{\cdot}16$, with 11 and 48 d.f.; $P > 0{\cdot}2$) so the weights of the groups after treatment were adjusted to the original weights and are expressed in Table 8 as mean increases in weight in milligrams per milligram of original weight.

The mean increases in weight of the larvae at pF 2·50 were grossly different from those at the other pF values. The latter were subjected to an analysis of variance based on weighted means because of the disproportionate numbers of

TABLE 7

MEAN pF VALUES OF SAND TO WHICH FIRST INSTAR LARVAE WERE EXPOSED DURING COURSE OF "DROUGHT" EXPERIMENT (SEE TABLE 6)

Time of Evaluation of pF Value	Mean pF Values		
At start of experiment	3·30	3·80	4·10
After 1 week	3·70	4·05	4·15
After 2 weeks	3·95	4·10	4·20
After 3 weeks	4·00	4·15	4·20
After 5 weeks	4·10	4·20	4·20

larvae surviving to be weighed in the different treatments (Snedecor 1946). The analysis suggested that the interaction of time and pF value of soil was highly significant ($F = 3{\cdot}93$, with 6 and 233 d.f.; $P < 0{\cdot}001$). Further analysis, using the interaction mean in place of the error mean square, suggested that the means of the pF values were not significantly different ($F < 1{\cdot}0$ with 2 and 233 d.f.; $P > 0{\cdot}2$) but that the means of the times were ($F = 39{\cdot}6$, with 3 and 233 d.f.; $P < 0{\cdot}001$). The standard errors of the differences of the means of the times and the observed differences between the means are also tabulated in Table 8. These suggest that the only significant difference between the means of the times was between the mean of 1 week and the means of the other times.

The changes in weight of the larvae at pF values of 3·30, 3·80, and 4·10 can be largely accounted for by periodic ingestion and excretion of soil by the larvae. The young larvae ingested considerable quantities of soil in their first week and their increases in weight in the first week were probably due mainly to the soil in their alimentary canals. These increases in weight occurred during the period in which the larvae made individual burrows away from the cells in the soil in which they had been placed. At the end of the second week most of the larvae looked like newly hatched larvae again, with little soil in their alimentary canals; so the significant decrease in weight after the first week was obviously due mainly to the voiding of soil previously ingested, and it occurred during the period in which the larvae seemed to have stopped burrowing.

The weights of the larvae between 2 and 5 weeks were very variable, with some larvae, even after 5 weeks, weighing as much as larva at the end of the first week. This variability probably accounts for the significance of the interaction

TABLE 8

MEAN INCREASES IN WEIGHT PER LARVA OF FIRST INSTAR LARVAE AFTER 1, 2, 3, AND 5 WEEKS IN SOIL AT FOUR pF VALUES

Weight increases expressed as mg mg original weight. Mean larval weight before experiment was 1·318 mg

Time (weeks)	pF 2·50†		pF 3·30		pF 3·80		pF 4·10		Mean of Times
	No. of Larvae	Increase in Weight	No. of Larvae	Increase in Weight	No. of Larvae	Increase in Weight	No. of Larvae	Increase in Weight	
1	38	2·2257†	32	0·9047	37	0·9651	37	0·9491	0·9413
2	38	4·3994†	25	0·4895	26	0·2987	19	0·3500	0·3807
3	‡	—	17	0·2582	10	0·4236	24	0·4784	0·3942
5	§	—	6	0·2865	4	0·3120	8	0·2959	0·2963
Mean of pF values				0·5912		0·6358		0·6320	0·6199

Analysis of Means

	Standard Errors of the Differences of the Means of the Times			Differences Observed between the Means of the Times		
	2 weeks	3 weeks	5 weeks	2 weeks	3 weeks	5 weeks
1 week	0·0628	0·0694	0·1039	0·5606***	0·5471***	0·6450***
2 weeks		0·0750	0·1077		0·1350	0·0844
3 weeks			0·1117			0·0979

*** Significant at $P < 0·001$.

† Control, not included in means of times and in the analysis of variance.

‡ Not weighed; many second instars.

§ Not weighed; all third instars.

mean square in the analysis of variance, and was probably due mainly to the periodic ingestion and excretion of soil, with the larvae being "in phase" at the end of the first week and being "out of phase" after that. Developing larvae, however, seem rarely, if ever, to void most of the soil in their alimentary canals

and tend to increase steadily in weight, although they probably vary considerably in weight from day to day. The larvae at pF 2·50, for example, did not show a loss in weight after the first week, and after 5 weeks they were all third instars. Even at 2 weeks the larvae at pF 2·50 were much heavier and were about three times as long as the larvae at the other pF values at 5 weeks, most of which still looked like newly-hatched larvae. Much of the difference between the larvae at pF 2·50 and the larvae at the other pF values was due to the fact that the former larvae extended their burrows to the surface of the soil and fed on the food to be

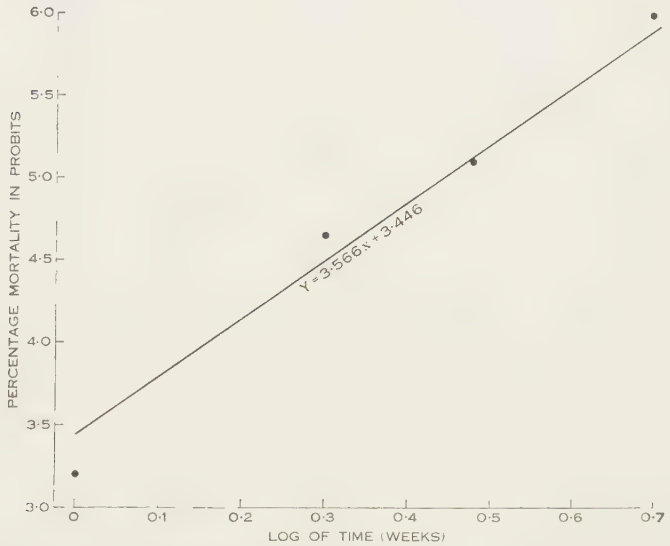

Fig. 3.—Effect of "drought" on the mortality of first instar larvae before migration to the surface.

found there whilst the latter larvae did not. The inability of the larvae in the dry soils to mature and increase in weight suggests, in fact, that the young larvae in dry soils, once having made their burrows, stay in their burrows and do not feed much until the soil is wetted.

In conclusion, since there is no evidence that the larvae in the above experiment died of water loss, the numbers of larvae alive at each interval of time can be combined to estimate the effect of the length of drought on the mortality rate of larvae. The relation between mortality in probits, corrected for mortality at pF 2·50, and the logarithm of time in weeks is shown in Figure 3; the calculated LD_{50} was 19·4 days, with 95% fiducial limits 17·2–21·6 days. Because of the artificiality of the experiment it is likely, however, that 19·4 days is an underestimate of the number of days of drought required to kill 50% of young larvae in the field.

(iii) *Mortality Rate of Larvae in Saturated Atmospheres.*—If starvation is the only important cause of deaths among first instar larvae living in soil that is so dry that they do not migrate to the surface of the soil and commence feeding, an

estimate of the effect of drought on the mortality rate of the larvae can also be obtained by measuring the death rate of larvae on moist filter paper, because on moist filter paper the larvae will not be exposed to desiccation. The following experiment was done to determine how long young larvae could survive without food in saturated atmospheres at different temperatures.

Thirty newly emerged larvae were kept at each of the temperatures 13·3, 15·8, 18·0, 20·3, and 21·8°C. Each larva was placed in a piece of straw standing on filter paper in a petri dish, the petri dishes were covered with black paper to reduce any irritation to larvae caused by light, and the pieces of filter paper were moistened each day. The percentage mortality of larvae every 4 days is given in Table 9.

TABLE 9

PERCENTAGE MORTALITY OF STARVED FIRST INSTAR LARVAE IN SATURATED ATMOSPHERES AT DIFFERENT TEMPERATURES

Temp. (°C)	Number of Days of Starvation						
	4	8	12	16	20	24	28
13·3	3	10	20	27	30	33	43
15·8	7	17	27	37	43	47	57
18·0	3	13	27	30	43	47	67
20·3	3	13	20	27	37	57	90
21·8	7	27	37	43	50	73	100

The percentage mortality at 18·0°C was plotted in probits against the logarithm of time. A regression line drawn by eye through the points gave an LD_{50} of 22·5 days. The similarity of the estimated LD_{50} to that of the previous experiment (19·4 days) suggests that starvation was, indeed, the most probable cause of larval death in the previous experiment. The data also indicate that the length of time which larvae can survive without feeding depends on the temperature.

(*c*) *Effect of Moisture on the Rate of Larval Development after Migration to the Surface*

After the larvae migrate to the surface of the soil they construct individual burrows about 1 in. long and feed on plant debris and other organic matter on the surface of the soil. Even at this stage larvae forage for food on the surface of the soil if food is scarce, but such foraging usually only occurs after rain, or perhaps after heavy dew.

Carne (1956) neatly demonstrated that older larvae only forage for food after rain, and there are many field observations which indicate that the rate of development of larvae generally is influenced by the frequency with which rain falls. For example, larvae from lawns and other places which are watered during dry spells are usually bigger and more advanced than larvae in pastures, and

they usually grow into bigger adults. Similarly, too, the larvae which complete their development early (by August) are large and become the biggest adults and emerge first. Larvae which do not complete their development till October feed less frequently because the number of rainy days per month decreases toward spring and evaporation increases. These larvae are usually small and become adults which emerge relatively late.

The maximum weight attained by the feeding larva was correlated with the weight of the prepua ($r = 0{\cdot}79$ with 24 d.f.; $P < 0{\cdot}001$), the weight of the prepupa was correlated with the length of the elytron of the adult ($r = 0{\cdot}81$ with 31 d.f.; $P < 0{\cdot}001$), and the length of the elytron was correlated with the fecundity of the female ($r = 0{\cdot}86$ with 20 d.f.; $P < 0{\cdot}001$). It is likely, therefore, that the fecundity of the adult is related to the food reserves of the larva. Hence the distribution of rain, by affecting the frequency with which larvae feed, probably affects the birth rate of the species in the field. This effect may well be considerable towards the drier limits of the distribution of the species in South Australia, but is unlikely to be a *major* factor influencing the numbers of *A. tasmaniae* in the higher rainfall area of the lower south-east of the State.

(*d*) *Effect of Drought on the Mortality Rate of Prepupae*

Prepupae are in diapause in their earthen cells during the early part of the summer. A considerable amount of water is lost from the soil at this time of the year and the water content of the soil may be near the wilting coefficient (pF 4·2) for many days or weeks.

Prepupae were expected to lose water in this period and it was thought that many prepupae would die in long periods of dry weather. Experiments were therefore conducted to determine (i) the rate at which prepuae lost water in unsatured atmospheres; (ii) the effect of loss of water on the mortality rate; and (iii) the influence of the cell on the rate of loss of water from the prepupae.

(i) *Rate of Loss of Water from Prepupae in Unsaturated Atmospheres.*— Initial experiments indicated that the percentage weight lost by prepupae in 20–24 hr was a linear function of saturation deficit at each temperature; these results are in agreement with those on other insects (Andrewartha and Birch 1954). To use laboratory data for forecasting water loss in the field it was desirable to know, however, if prepupae lost the same amount of water if exposed to equal products of saturation deficit and time at the same temperature, and hence the following experiment was done.

Prepupae were placed in glass jars in which humidities were controlled with sulphuric acid–water mixtures (Solomon 1951). The insects were placed on a piece of wire gauze $\frac{1}{2}$ in. above the surface of the acid in any jar and their losses in weight determined by weighing them individually before and after treatment.

The experiment was designed so that there were 12 treatments in two series of six at 13°C, which approximates the soil temperature in the field in October–November. In one series prepupae were exposed to saturation deficits of 0, 1, 2, 3, 4, and 4·5 mm Hg for 5 days, and in the other series prepupae were exposed to

TABLE 10

MEAN PERCENTAGE WEIGHT LOSS OF PREPUPAE IN RELATION TO THE PRODUCT OF SATURATION DEFICIT AND TIME

Mean weight of a prepupa before the experiment was 113·7 mg

Saturation Deficit (in mm Hg) × Time (days)	2½-day Series			5-day Series			Comparing Series (direct test)		
	No. of Insects Used	Mean Weight Loss (%)	Variance	No. of Insects Used	Mean Weight Loss (%)	Variance	S.E. of Means	Total D.F.	t
0	50	4·2	9·04	50	8·6	6·10	0·550	98	8·00***
5·0	71	16·3	20·66	76	12·8	14·28	0·688	145	5·09***
10·0	79	30·0	57·20	72	22·5	98·57	1·429	149	5·25***
15·0	79	41·3	52·95	71	25·6	107·94	1·597	148	9·83***
20·0	77	50·2	91·06	84	33·7	117·02	1·614	159	10·22***
22·5	73	53·4	84·20	71	39·3	104·96	1·620	142	8·70***

Analyses of Variance for Regression

Analysis	Source of Variation	D.F.	S.S.	M.S.	F
Mean percentage weight lost in relation to equivalent products of saturation deficit and time (linear regression)	Difference in regression co-efficients	1	8,931·2	8,931·2	124·2***
	Distance between regression lines	1	20,213·6	20,213·6	281·1***
	Total difference between regression lines	2	29,144·8	14,572·4	202·6***
	Residual about regression lines	849	61,050·8	71·9	
Significance of departure from linear regression for the data of the 2½-day series of the regression: $y = 0{\cdot}033x^2 + 2{\cdot}986x + 3{\cdot}366$	Deviations from linear regression	427	27,170·39		
	Deviations from curvilinear regression	426	26,100·75	61·27	
	Curvilinearity of regression	1	1,069·64	1,069·64	17·46***
Significance of departure from linear regression for the data of the 5-day series of the regression: $y = 0{\cdot}013x^2 + 1{\cdot}041x + 8{\cdot}379$	Deviations from linear regression	422	33,883·8		
	Deviations from curvilinear regression	421	33,726·4	80·1	
	Curvilinearity of regression	1	157·4	157·4	1·97*

* $P > 0{\cdot}05$. *** $P < 0{\cdot}001$.

saturation deficits of 0, 2, 4, 6, 8, and 9 mm Hg for $2\frac{1}{2}$ days. The insects in each series were thus exposed to 0, 5, 10, 15, 20, and 22·5 mm (evaporation × days), and any treatment in one series was directly comparable with a treatment in the other series.

The mean percentage weight lost at each treatment is given in Table 10 and is plotted against the product of saturation deficit and time in Figure 4. The

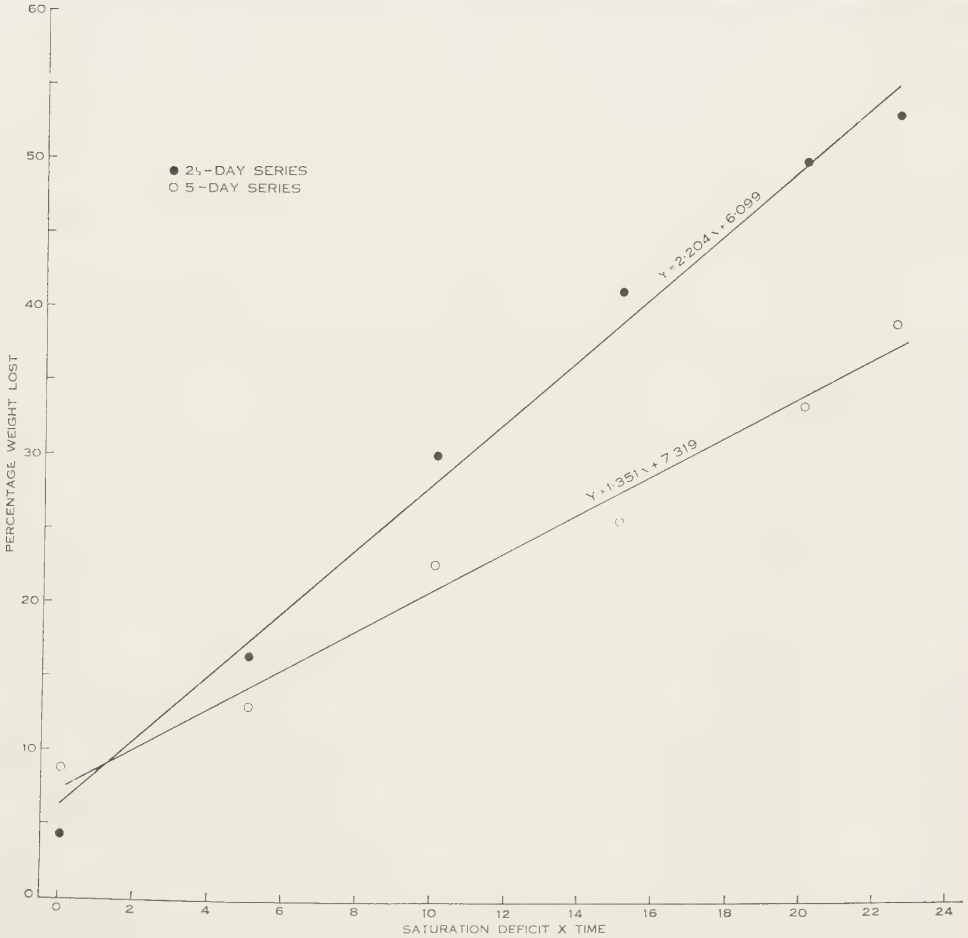

Fig. 4.—Mean percentage weight lost by prepupae in relation to the product of saturation deficit and time. Linear regression equations have been fitted to the data.

variances of the percentage weight lost at each treatment are also given in Table 10; as in initial experiments the variances are roughly proportional to the means, and Bartlett's test of homogeneity of variances (Snedecor 1946) indicates that the variances are markedly heteroscedastic. If the mean percentage weights lost are to be used in a regression analysis a homoscedastic transformation must be applied to the data. A regression analysis on the untransformed data can be done, however, if the total sum of squares is obtained from the deviation of the percentage

weight loss of each insect from the general mean (Fisher 1936). This method was used.

Regression analysis of the data suggested, however, that the percentage weight lost in the $2\frac{1}{2}$-day series was not a linear function of the product of saturation deficit and time (Table 10). It was considered preferable, therefore, to compare the mean percentage weight losses of the groups in the two series directly by using their standard errors. The values of t (Table 10) indicate that the prepupae in the $2\frac{1}{2}$-day series lost more weight than the prepupae in the 5-day series at each level of evaporation, except over water.

It is probable that the weight lost by the prepupae over water was due to excretion because the insects were observed to excrete drops of a watery fluid, particularly when disturbed or handled. Similarly, it is probable that the loss in weight of insects in unsaturated atmospheres includes some excretion, but is nevertheless all, or nearly all, water.

It is also probable that excretion accounted for a larger proportion of the percentage weight lost in the 5-day series than in the $2\frac{1}{2}$-day series and that the differences between the two series in the amounts of water lost by transpiration were even greater than are apparent from the data.

(ii) *Effect of Loss of Water on the Mortality Rate of Prepupae.*—To estimate the effect of drought on the mortality rate of prepupae it was necessary, after having obtained estimates of the rate of loss of weight by the insects in unsaturated atmospheres, to determine the effect of weight loss on the mortality rate and to determine whether the loss of equivalent amounts of weight at different rates affected the mortality rate.

A disturbing feature of initial experiments was the wide range in percentage weight lost at each saturation deficit, particularly at the higher ones. This variability can be neglected statistically when estimating the effect of weight lost on the mortality rate because the probit analysis is not complicated by the inequalities of the variances of the points along the horizontal axis. Any such analysis is, however, biologically unsound unless the range of weight (water) lost by groups of insects is small and is constant. Therefore, in this experiment only prepupae whose weight losses fell within narrow limits were used to estimate the mortality rate.

The experiment was a continuation of the one previously described. The weight losses of the insects at each level of desiccation in the $2\frac{1}{2}$- and 5-day series were distributed approximately normally with mean weight losses shown in Table 10. A mean weight loss slightly higher than that in Table 10 was chosen for each group of insects at a particular level of evaporation and the insects were desiccated further, if necessary, and weighed every 4 hr until a number of the individuals in the group had each lost $y_i \pm 1{\cdot}5\%$ of their original weights, where $\bar{y}_i$ was the selected mean percentage weight loss for the group.

Two series of insects were therefore again obtained, one in which insects had lost $\bar{y}_i$ $(i = 1, 2, \ldots, 6) \pm 1{\cdot}5\%$ of their original weights in $2\frac{1}{2}$–$3\frac{1}{2}$ days (mean = 3 days) and one in which insects had lost $\bar{y}_i$ $(i = 7, 8, \ldots, 12) \pm 1{\cdot}5\%$

of their original weights in 5–7 days (mean = 6 days). Any individual in any group was discarded if the amount of weight it lost did not fall within the limits arbitrarily selected for the group. The two series are henceforth called the 3- and 6-day series.

After having been desiccated the prepupae were placed on moist blotting-paper and allowed to absorb water before being placed in individual burrows in moist soil. It was thought that prepupae treated in this manner would have a chance to recover, at least partially, before expending energy in constructing a cell in the soil. The effect of weight loss on the mortality rate might then be more akin to

TABLE 11

RELATION BETWEEN THE PERCENTAGE WEIGHTS LOST BY PREPUPAE AND THE NUMBERS THAT DIED 10, 20, 30, AND 40 DAYS AFTER DESICCATION

Insects Used	Mean Weight Lost (%)	10 Days		20 Days		30 Days		40 Days	
		No. Used	No. Dead	No. Used	No. Dead	No. Used	No. Dead	No. Used	No. Dead
3-day series*	4·2	29	0	29	0	28†	1	28	1
	18·2	50	3	50	3	49	3	48†	4
	33·0	39	1	39	1	38†	1	38	2
	48·1	32	20	32	21	31†	21	31	22
	55·0	41	38	41	38	41	39	41	39
	59·6	34	34	34	34	34	34	34	34
6-day series*	8·6	50	1	50	1	50	2	50	2
	17·8	48	2	48	2	46†	3	46	3
	32·7	40	1	39†	2	39	3	37†	4
	39·0	29	2	28†	2	28	2	26†	2
	45·4	39	8	38†	9	38	12	36†	14
	51·0	32	12	31†	16	29†	19	29	22

* See pp. 192–3 for definition.

† The changes in the numbers used are due to the exclusion of deaths due to *Cordyceps aphodii*.

natural conditions in which a prepupa does not have to construct a new cell after being desiccated. The number of prepupae dead in each selected group 10, 20, 30, and 40 days after desiccation were then recorded.

There was no correlation between the amounts of water absorbed by the insects after desiccation and the subsequent survival or death of the insects; the mortality rate seemed to be a function only of the amount of weight initially lost. The mean percentage weight loss (y_1) for each selected group of insects, the numbers of insects whose weight losses fell within the limits $y_1 \pm 1{\cdot}5\%$, and the mortalities of these insects, excluding deaths due to the fungus *Cordyceps aphodii*, after 10, 20, 30, and 40 days are given in Table 11. The relation between weight loss and mortality rate is shown for each series of insects in Figure 5.

The outstanding feature of the results, as indicated in Figure 5, was that one mortality curve did not give as good a fit to the data as a combination of two curves to cover different parts of the range of weight loss; this distinction between different parts of the weight loss range was obscured in earlier experiments by the variability in weight loss within groups of insects. The mortality of prepupae in this experiment was not influenced to any extent by weight loss up to 33–40%, but rapidly increased with relatively small increments of weight loss above about

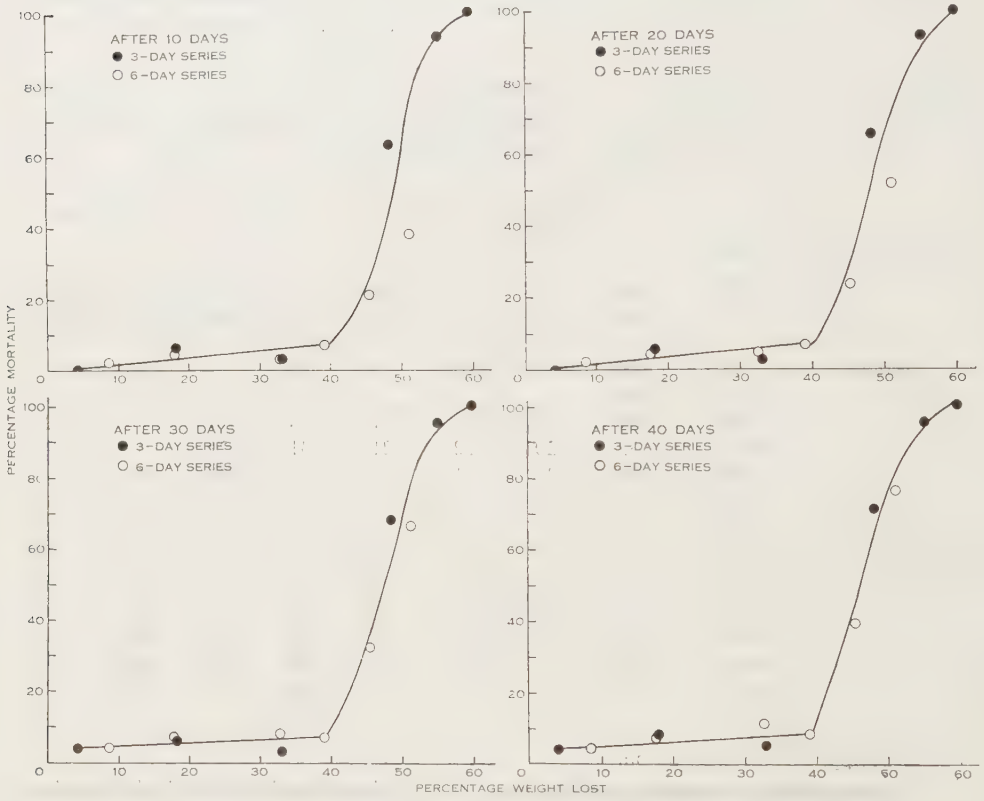

Fig. 5.—Effect of the percentage weight lost by prepupae on their mortality.

40%. Similar data have been recorded for larvae of *Cephus cinctus* Nort. (Salt 1946), larvae, prepupae, and pupae of *Popillia japonica* Newman (Ludwig and Landsman 1937), and eggs of *Calandra oryzae* L. (Birch 1944).

Two groups of prepupae in each of the series lost about the same weight at different rates (18·2 and 33% in the 3-day series, and 17·8 and 32·7% in the 6-day series), but there was no difference in mortality between the series which could be attributed to the rate at which the insects lost weight. However, the mortalities of insects which had lost more than 39% of their weight suggests that the rate of weight loss did have some initial effect on the mortality rate. The mortalities of both series of insects above this limit (39% weight loss) can be

fitted to a single mortality curve at each interval of time, but the fit becomes progressively better as time increases. This is due largely to an increase in mortality with time in the 6-day series. The scarcity of points does not, however, permit the difference between the two series to be tested statistically.

Pupation was retarded when prepupae lost more than about 25% of their original weight and some insects which died between 10 and 40 days died when pupating. The increase in mortality with time emphasizes the warning by Andrewartha and Birch (1954) that the influence of water loss on the mortality rate may not be immediate and that time is an integral part of any mortality data. After 40 days there was little or no apparent difference in the mortality rate of prepupae in the two series; similarly the mortality rates of larvae of *Popillia japonica* and of *Cephus cinctus* were not affected by the rates at which the insects lost water (Ludwig and Landsman 1937; Salt 1946).

Since there was no apparent difference in the mortality rate of prepupae of *A. tasmaniae* in the two series after 40 days, it is likely that if prepupae had lost 39·0% of their weight in 3 days they would not have died in any larger numbers than in the 6-day series. A weight loss of 39% has, therefore, been taken as the limit above which the mortality rate of the prepupae increased in both series, and using combined results for the two series it was estimated that a weight loss of 45·9% (95% fiducial limits = ±1·9%) would be necessary to kill 50% of the prepupae after 40 days.

The water content of the insects averaged about 77% at the start of the experiment, so if it is assumed that the weight loss was water loss it can be said that there was a sharp increase in the mortality rate when the water content of the larvae fell below about 62% and that 50% of the insects died when their water content fell to about 57%.

(iii) *Influence of the Cell on the Rate of Loss of Water from Prepupae.*— The cell of the diapausing prepupa is not lined with wax, but it was considered possible that a biological membrane of some kind — perhaps proteinaceous — was secreted on its inner surface and enhanced the chance of survival of the larva by reducing the permeability of the cell wall to water vapour. To test this hypothesis, simple evaporimeters were constructed from portions of cells constructed by prepupae. The permeability of the inner surfaces of the cells to water vapour was then measured.

A schematic diagram of an evaporimeter is given in Figure 6. The following evaporimeters operated as controls:

(1) Evaporimeters made from artificial cells (i.e. cells carved out of dry soil to the size, shape, etc. of the natural cells).
(2) Evaporimeters consisting of glass tubing open at the top end.
(3) Evaporimeters made with natural cells but filled with a saturated solution of sodium chloride.

There were four replicates of each type of control evaporimeter and three evaporimeters constructed from natural cells. Powdered potassium permanganate placed at the bottom of each evaporimeter indicated from time to time that certain

evaporimeters were leaking. The bottoms of these evaporimeters were resealed and the resultant excess water losses in those intervals of time were not included in the analysis of the results.

The mean increments of water loss in millilitres per square centimetre of evaporative surface for each type of evaporimeter at each interval of time are given in Table 12. The losses of water from the open tubes were clearly much

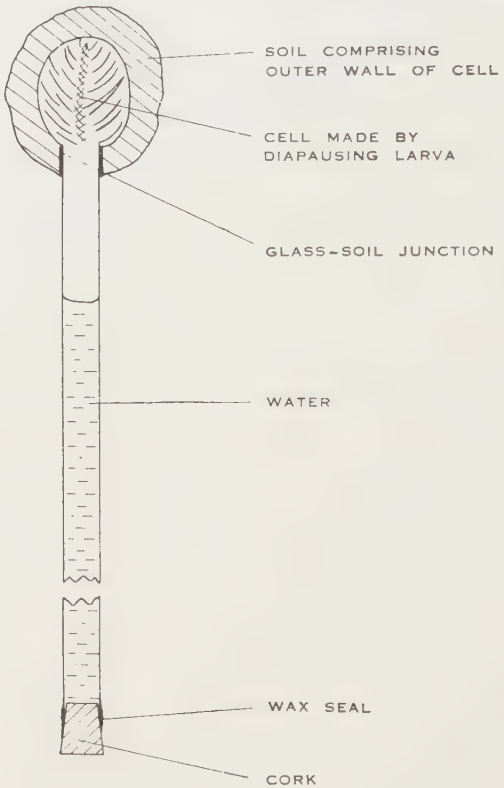

Fig. 6.—Schematic diagram of the system used to measure the permeability of the cell wall constructed by the diapausing prepupa.

greater than those from the other evaporimeters and were excluded from the analysis of variance which indicated that there was no significant difference in mean water loss from the other evaporimeters ($F = 2{\cdot}49$ with 2 and 43 d.f.; $P > 0{\cdot}05$).

The control evaporimeters which contained a solution of salt were expected to lose less water than those with water. This they did, but the differences were not significant. The method, therefore, was fairly crude. Nevertheless, if there was a difference between artificial and natural cells it should have been sufficiently large to have been detected in the experiment. It is probable, therefore, that

there is no biological lining of the prepupal cell which influences the rate at which water passes out of the cell.

(e) *Lethal Influence of Excess Water*

First instar larvae, particularly before feeding, have often died in the laboratory when the soil has been too wet and the larvae have been held by the surface tension of water, and observation suggests that young larvae may similarly die in the field if unseasonal rains occur. However, excess water occurs most frequently in June–September and affects particularly the mortality rate of the third instar larvae. So the following discussion pertains mainly to third instar larvae.

TABLE 12

MEAN INCREMENTS OF WATER (ML/SQ. CM EVAPORATIVE SURFACE) LOST FROM VARIOUS TYPES OF EVAPORIMETERS

Type of Evaporimeter	Intervals of Time						General Mean	Total No. of Observations
	1	2	3	4	5	6		
Natural cells–water	0·30	0·30	0·41	0·31	0·17	0·55	0·344	17
Natural cells–salt solution	0·21	0·36	0·30	0·12	0·13	0·47	0·259	20
Artificial cells–water	0·27	0·30	0·44	0·22	0·12	0·42	0·293	24
Open tubes–water	2·28	3·17	3·97	2·38	0·92	3·57	2·717	20

Excess water influences the mortality rate of third instar larvae by (i) drowning the insects, or (ii) promoting infection with pathogenic organisms such as the entomophagous fungus *Cordyceps aphodii*.

Flooding occurs regularly every winter on the flats between the ranges in the south-east of the State but in some years is more extensive than in others. Flooding drowns larvae of *A. tasmaniae* or exposes them to predators and other unfavourable environmental influences. In flooded areas the majority of larvae come to the surface of the soil within 24 hr of flooding and lie in a comatose state near or on the surface. Birds such as seagulls, white ibis, and magpies have often been observed feeding on such larvae in flooded areas.

Some larvae may survive in flooded areas; some have been observed to float to the surface of the water and finally reach dry land and some larvae have been observed to have survived in dung pads which were not covered with the flood water. The larvae, however, have never been seen climbing up pieces of vegetation as larvae of *Oncopera fasciculata* Walker do in flooded areas (Madge 1957), and very few survive if the flood water persists for many days. To determine how long

larvae could survive immersion in water the following laboratory experiment was done.

Larvae were immersed in water at 8 and 16°C for 4, 8, 16, 20, 24, and 48 hr. They were then placed in burrows in moist soil and the numbers dead were recorded 22 days later. Eighty larvae were used for each treatment but those infected with *Cordyceps* were omitted from the results.

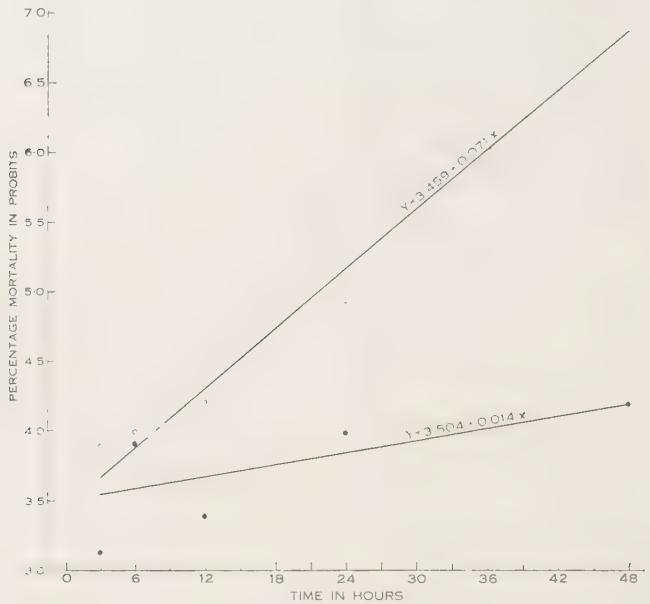

Fig. 7.—Percentage mortality of third instar larvae after immersion in water at two temperatures.

The percentage mortality in probits is plotted against time of immersion in Figure 7. It is evident that temperature had a marked effect on the mortality rate. The LD_{50} at 16°C was calculated to be 21·7 hr, with 95% fiducial limits = ±4·4 hr, but more than 50% of larvae survived being immersed in water at 8°C for 48 hr; temperature similarly affected the mortality rate of larvae of *Heliothis armigera* (Hbn.) (Barber and Dicke 1939).

The mean temperature of flood water in winter at Mt. Gambier is about 8°C, so larvae in the field would be able to tolerate immersion for more than 48 hr, and field observations suggest that water must persist for more than 3 days to kill a large proportion of the insects.

IV. Discussion

The eggs of *A. tasmaniae* can absorb water from soil within the approximate range of pF 2·5–3·75 and are probably capable of absorbing water some 6–10 days after being laid in the field. The tendency of the adults to emerge from the soil

only after rain and to lay eggs within the range of pF 2·8–3·2 (Maelzer 1961) makes it difficult, however, to obtain evidence of the differential survival of eggs in relation to moisture in the field. Certainly in wet summers, when the adults emerge after 0·8 in. or more of rain, the soil would remain moist enough for eggs to complete their development. In dry summers, however, adults may emerge after only 0·3–0·4 in. of rain and no further rain may fall whilst the eggs are in the soil; in such years the soil may dry out so much that the eggs may not be able to complete their development.

To estimate the chance of eggs dying in dry summers, soil samples were taken from a terra rossa (clay loam) near Mt. Gambier on March 24, 1956, 3 weeks after 0·4 in. of rain had fallen. The percentage water content of 12 samples, which were taken at a depth of 8 in. from each of three stations under a bare surface ranged from 15·0 to 18·0, mean 16·6. The range for 12 similar samples from under grass stubble was 10·6–14·4%, mean 12·0. The difference between the means was significant (S.E. of difference = 0·47, $t = 9{\cdot}81$, $P < 0{\cdot}001$). The equivalent pF values for the means were 3·70 under a bare surface and 4·05 under stubble. Eggs laid in the soil under the bare surface would, therefore, on the average, have been able to absorb water and develop whilst those laid under stubble would have died.

Particularly after dry summers, larvae of *A. tasmaniae* are found in winter only in areas whose surfaces were bare in summer. This can be explained by differential egg laying by the adults or by differential survival of the eggs under bare surfaces and under grass stubble. There is no evidence to distinguish between these two possibilities, but in view of the behaviour of the adult (Maelzer 1961) it is considered more probable that the distribution of larvae after dry summers is the result of differential egg laying under different pasture surfaces, and it is tentatively concluded that moisture has little effect on the mortality rate of the eggs because the eggs tend to be laid in places where moisture is not a limiting factor.

It is also concluded that drought in summer has little or no effect on the mortality rate of the diapausing prepupae. During the course of this study very few dead prepupae were found whose deaths could possibly be attributed to desiccation in summer. In the absence of an empirical relation between the duration of drought and the mortality rate of insects in the field, estimates can be made from laboratory data of the duration of drought required to kill any proportion of the prepupae. Since the cells the prepupae make in the soil do not seem to influence the rate of water loss, such estimates can be based on (1) the ability of the insects to tolerate water loss, and (2) the rate at which the insects lose water in unsaturated atmospheres, taken from the data of the 5-day series.

The ability of the prepupae to tolerate water loss fell off rapidly after their water contents fell below 62%, and it was estimated that 50% of the insects died when their water contents fell to 57%. The water contents of the insects fell to these limits after exposure to 22·5 and 28·5 (extrapolated) mm of (evaporation × days) respectively. Allowing that soil at 20°C and at pF 4·20 is in equilibrium with air at 98% R.H., i.e. a saturation deficit of 0·35 mm Hg, it is estimated that

64 and 81 days' drought of this particular severity would be required in the field for the water contents of the insects to fall to 62% and 57% respectively.

Prepupae, however, did not lose equivalent amounts of weight when exposed to equal products of saturation deficit and time, but lost less weight when exposed to a lower saturation deficit for a longer time. Since the total evaporation required in the field to desiccate the prepupae is the product of a very low saturation deficit and a very long time, it is probable that the insects in the field will lose water less slowly than they did in the laboratory. The above estimates of the duration of drought required to produce certain effects in the field are probably, therefore, underestimates. Nevertheless they are useful approximations because droughts of even their severity and duration have never been known to occur in the lower south-east of South Australia.

In contrast to those of the egg and the diapausing prepupa, the mortality rate of first instar larvae is likely to be markedly affected by moisture in the field. The young larvae, after hatching from the eggs, do not seem to migrate to the surface of the soil and start feeding until the soil around them is wetter than pF 3·0. Since the eggs hatch 4–5 weeks after they are laid, the soil around the young larvae has often dried out considerably when the larvae emerge, and the larvae do not migrate to the surface until the soil is saturated with rain. The time until such rain falls constitutes the period of "drought" during which the larvae feed a little but ultimately die, probably of starvation.

The length of this period of drought varies considerably from year to year and has been estimated to range from 0 to 72 days between the years 1927 and 1956. Since it was estimated that about 30 days of drought one year killed 50% of the young larvae it is considered that the duration of this autumn drought, which is often terminated by the break of the season, is one of the major factors influencing the numbers and distribution of *A. tasmaniae*.

This study suggested that the wetness of winter was also a major factor influencing the numbers and distribution of *A. tasmaniae*. Excess moisture in winter may simply drown larvae or may promote infections with pathogenic organisms, particularly *Cordyceps aphodii*.

Flood water may persist for many days if it results from a rise in the water-table; it drains away after 1–2 days if it is the accumulation of run-off. On terra rossa soils and on sandy ridges, flooding may occur as the result of run-off, and on these well-drained soils flooding has little direct effect on the mortality rate of larvae. On poorly drained soils, however, and particularly on low-lying meadow podsols, flood water may persist for many days or weeks; in the wet winter of 1955 very large numbers of larvae were drowned following extensive flooding on these soils.

There were indications that bacterial infections of *A. tasmaniae* also increased with excess water in soil and it is probable that excess water usually weakens larvae so that they succumb more readily to diseases and other components of the environment. The other major cause of death amongst larvae in wet winters was, however, infection by *C. aphodii*.

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REPRODUCTIVE BEHAVIOUR OF THE MARSUPIAL MOUSE, *ANTECHINUS FLAVIPES* (WATERHOUSE) (MARSUPIALIA) AND THE DEVELOPMENT OF THE POUCH YOUNG

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Summary

Techniques for the capture and maintenance of *Antechinus flavipes* in the laboratory are described.

Reproduction is restricted to early August when protracted copulation of more than 5 hr occurs.

The young are born early in September after a mean gestation period of 31·5 days. The average litter size is 6·8. The neonatus has a well-developed head and fore limbs while the posterior end of the body is strongly flexed ventrally. Only rudiments of the hind limbs are present. The crown–rump length of a neonatus is 4·9 mm and its weight 0·0164 g. The development and growth of the pouch young are described. Sex can be determined at an age of 25 days and the eyes open at about 62 days. Suckling continues for 90 days and sexual maturity is probably achieved after 320 days in the August following birth.

The neonatus of *A. flavipes* and features in its development are compared with other marsupials and a placental, *Mus musculus,* of comparable dimensions. The slow reproduction rate and difficulty in handling do not recommend *A. flavipes* as a possible laboratory animal.

I. Introduction

Several studies on the reproduction and development of marsupials have been conducted during the past decade. These include investigations on opossums (Reynolds 1952), bandicoots (Lyne 1952), phalangers (Tyndale-Biscoe 1955; Dunnet 1956), and macropods (Sharman 1955). The carnivorous marsupials, Dasyuridae, on the other hand, have received scant attention, the most significant work on this group being that on the native cat, *Dasyurus quoll* (Hill and O'Donoghue 1913; Hill and Hill 1955). This paper gives details of the reproduction of one of the smaller species of the Dasyuridae, the yellow-footed marsupial mouse, *Antechinus flavipes* (Waterhouse, 1838).

The broad-footed marsupial mice (*Antechinus*) are included with several other genera of small carnivorous or insectivorous marsupials such as *Phascogale, Planigale,* and *Sminthopsis* in the subfamily Phascogalinae, all of which are characterized by the retention of three premolars in each jaw. There are about 10 species in the genus *Antechinus* which is distributed through the Australian mainland, Tasmania, and New Guinea (Tate 1947).

A. flavipes occurs from north Queensland south through New South Wales and Victoria to South Australia and in the south-west of Western Australia. It is

* Australian Museum, Sydney.

abundant in New South Wales, and occurs both in rain-forest and in dry eucalyptus forest (Marlow 1958). It is particularly plentiful in the vicinity of Sydney, where it lives in wind-worn caves in the rock outcrops of the typical Hawkesbury sandstone country with a predominantly dry eucalyptus forest vegetation. Adult males have a total length of 210 mm, a tail length of 90 mm, and weigh 45 g while adult females have a total length of 175 mm, a tail length of 80 mm, and weigh 31 g (Plate 1, Fig. 1).

II. Methods and Materials

The present study extended from August 1956 to December 1959, during which time 19 specimens, 8 males and 11 females, were trapped alive and kept in captivity. Six litters involving a total of 41 juveniles were born in captivity. Four of these litters resulted from observed laboratory matings, while two females were trapped in a pregnant condition.

(*a*) *Capture*

The animals were captured in small wooden-box traps which were 9 in. long and 2 in. square internally. The most satisfactory bait was found to be raw bacon. All the animals were captured in sandstone caves or under rock slabs where signs of their activity in the form of footprints and faeces were plentiful. Metal traps such as the "Longworth" (Chitty and Kempson 1949) proved unsatisfactory, due possibly to their shiny nature and slippery floor. The efficiency of small traps in sandstone caves is at variance with the experience of Horner and Taylor (1959) who were working in approximately the same area and in similar terrain. The majority of the animals captured in the present study were trapped at Narrabeen, on the coast of New South Wales about 15 miles north of Sydney (33°42′S., 151°17′E.).

(*b*) *Housing*

A. flavipes is extraordinarily fast and agile in its movement and special escape-proof cages were designed to house specimens in the laboratory. These consisted of wooden boxes 24 in. long, 10 in. wide, and 9 in. deep and which were divided into two equal compartments by a vertical partition at right angles to the long axis. A hole 3 in. in diameter, which could be closed by a horizontally sliding shutter, at the base of this partition allowed access from one compartment to the other.

The front of each compartment was closed by a plate of glass which slid into vertical grooves. Wooden grooves were attached to the outside of the cage at each end, and a nest-box measuring 5 in. on each side fitted into them. Access from the nest-box to the main compartment was possible through further holes 3 in. in diameter at each end of the main cage. Each nest-box could be closed by a metal shutter which slid in vertical grooves and each had an inspection panel at the rear covered with $\frac{1}{2}$ in. wire netting beneath a removable wooden cover.

Each member of a breeding pair was housed at either end of the assembly described above, and controlled mating could be carried out by allowing them to

pass to each other through the aperture in the central partition. It was also possible to lock the animals into their nest-boxes when the main part of the cage was being cleaned or when food or water were being introduced. The nest-boxes could be removed entirely from the main cage and could be used as transport containers or interchanged with those of other cage assemblies.

(*c*) *Handling*

Under normal circumstances the animals could be urged through the various sliding partitions in the cages and this reduced the necessity for much handling. Similarly the animals could be examined by locking them in the nest-box which was then removed from the cage assembly. Adequate inspection of the shallow pouch area of the females was possible by removing the cover at the rear and tipping the box so that the ventral surface of the animal was pressed against the wire netting of the inspection panel. A blunt seeker was then introduced through the wire and used to move the fur gently to one side to facilitate examination of the pouch young.

Weighing and measuring necessitated handling which was effected by driving the animal from the nest-box into a cloth bag with a draw-string round the neck. The marsupial mouse was forced into a corner of the bag by gentle pressure and this corner was enclosed in the palm of the left hand while the animal's tail was grasped through the bag. The bag was opened with the right hand which was then inserted to grasp the tail itself. The bag was peeled forward over the animal until the requisite portion of its body was exposed. The animal normally remained quiet provided that its head remained covered. Females showed far less inclination to bite than did males during these operations. It was found inadvisable to hold the animal by the scruff, since the skin of the neck is rather fragile and large tufts of hair are liable to be detached. The strict precaution of maintaining a firm grip on the tail during the whole of the handling period was most necessary since if the animal managed to escape in the laboratory extreme difficulty was experienced in its recapture.

(*d*) *Diet in Captivity*

The natural diet of *A. flavipes* consists mainly of invertebrates, although carrion is also eaten (Le Soeuf and Burrell 1926). It was not possible to keep up a regular supply of insects for feeding purposes, so the animals were fed on the carcases of adult laboratory mice which had been killed previously and kept under refrigeration. Drinking water was supplied in shallow dishes. Mealworm larvae (*Tenebrio molitor*) were supplied very occasionally to supplement this diet. An adult male which was captured in July 1958 lived for two years on a diet of dead laboratory mice and water.

(*e*) *Weighing and Measuring.*

Pouch young of known age were detached at 5-day intervals from the pouch area while the adult female was enclosed in a bag as described above. Only one juvenile was removed on each occasion. Measurements (mm) of its crown–rump,

tail, and hind foot lengths were taken with a pair of blunt-pointed dividers and the animal was then weighed to the nearest milligram. A record was made of the stage of development of its major external features prior to fixation in 80% alcohol. One litter was retained intact and examined at weekly intervals. Considerable difficulty was experienced in measuring them in their early stages due to their small size and active movements, nor was it possible to weigh them while they were firmly attached to the teats. Attempts were made to mark each individual in the pouch so that a record of its growth could be kept, and although spots of gentian violet, fuchsin red, and "Duco" were applied to various portions of their bodies, all these marks were cleaned off by the mother. As these young grew older and relinquished the teats temporarily, it was possible to enclose them alive in a small cardboard box and weigh them to the nearest gram. Two operators were needed to measure these young alive. One held the animal supine in the palm of his left hand with the head pressed back with a thumb under the chin and the tail extended by the right hand. The other operator then measured the total length from the tip of the nose to tail with blunt dividers and the tail length from the centre of the cloaca to the tail tip. The head and body was then measured from the tip of the nose to the centre of the cloaca and the hind foot from the heel to the end of the longest claw. It was not practicable to measure ear length since the animals were able to contract the pinna appreciably.

Variations in the degree of flexion of the trunk during measurement caused unavoidable errors in the values obtained for head and body length. Minor damage to the tail tip of some individuals during measuring also caused discrepancies.

During 1958, the females, from whose pouches young were being removed at 5-day intervals, killed the remainder of their litters when they were about 40 days old. This may have been due to excessive handling and interference. Individuals of the only litter reared in 1959 were removed after 40 days and the time interval extended to 10 days to conserve specimens.

III. Reproductive Behaviour

Although marsupial mice were kept throughout the year and were given frequent opportunities to copulate, mating occurred only during a restricted period at the beginning of August. Lack of specimens precluded histological examination of ovaries, but observed copulations would indicate that oestrus lasts for an average of 4·3 days, with a maximum of 7 and a minimum of 2 days. One female was secluded from the male after the initial copulation and mated again with him when he was introduced 26 days later. This isolated case may have been due to a recurrence of oestrus and indicates the possibility of copulation during advanced pregnancy, as a litter was born 5 days after the second copulation.

(*a*) *Courtship and Copulation*

Courtship is initiated by the male seizing the scruff of the female's neck in his jaws and following her round the cage. While still maintaining his grip, the male maneouvres the female into a position which permits his mounting from

the rear. The males are very powerful and on one occasion one was observed to lift the female off the floor while suspended only by his hind feet from the wire wall of the cage. Courtship lasts for about half an hour and merges gradually into the initial stages of copulation. Erection occurs during the final stages of courtship and when the male has finally mounted the penis is strongly flexed and has a markedly bifid glans.

Copulation is of long duration, lasting for more than 5 hr, and exhibits sharply defined quiescent and active phases. Throughout copulation the fore limbs of the male are flexed posteriorly below the thorax, maintaining a grip on the flanks of the female in the anterior lumbar region. During the quiescent period, the male releases the scruff of the female and may exhibit a scratching reflex with one of his hind feet. In the early stages the penis may be withdrawn and the male may turn his head and groom his genital region. As copulation proceeds, the flexure in the penis disappears and the phallus then passes to one side of the scrotal peduncle. At this stage the animals become firmly locked together in a manner similar to that which obtains in certain carnivores.

The onset of the active phase is heralded by a remarkable sinuous lateral wriggling of the tail of the male who then seizes the female's scruff in his jaws. He braces his hind feet against the female's rump and gives a single powerful coital thrust. Both animals roll over onto one side together and then resume their former position. This active phase lasts for about 10 sec and alternates regularly with the quiescent stage which lasts for about 4 min.

The females mated on the average on three occasions during their oestrous period, with a minimum of two and a maximum of four. This behaviour differs from that of *Dasyurus* (Hill and O'Donoghue 1913) which will not copulate more than once in a season. The role of the female during copulation is entirely passive: in the later stages she squats with her hindquarters slightly raised and with her head flexed downwards so that the crown rests on the floor of the cage. The courtship advances of the male are strongly resisted by the anoestrous female who utters high-pitched squeaks and rolls over on her back when seized. A scuffle normally then ensues in which the male may bite the female about the head and neck. Under favourable circumstances contact between the two animals is then broken. The behaviour of the male is extremely savage, particularly during the early stages of courtship, and, of two uncooperative females, one was so badly injured by the male that she died on the following day, while the other had the whole of her scalp torn off by the male who had seized her by the top of her head. The situation in these two cases was probably aggravated by the inability of the female to escape.

(*b*) *Pouch Development*

Throughout most of the year the pouch area of *A. flavipes* is discernible only as a region on the ventral surface which bears fine white hairs and minute teats. The first signs of pouch development occur about 16 days before parturition when the lateral walls begin to thicken. At maximum development, the pouch area has raised edges about 5 mm high and consists of an equilateral triangle

about 3 cm on each side with its apex directed caudally. The interior of this depression is sparsely haired and contains two rows of four teats lying parallel to the raised edges, while the floor itself may be divided by a shallow, vertical, median ridge. This state of maximum development extends from 4 days before parturition to about 35 days after weaning when gradual atrophy commences. Similar pouch hypertrophy also occurs in the unmated female and after sterile copulation. It is therefore presumed that ovulation is spontaneous and that pouch development is controlled by the action of progesterone from the corpora lutea. This phenomenon in *A. flavipes* may be comparable with pseudopregnancy among some Eutheria.

(*c*) *Gestation*

The pouch areas of the females were inspected twice daily after the first mating so that the day of birth could be determined. An average gestation period of 31·5 days, with a maximum of 33 and a minimum of 30 days, was obtained from four litters which were born in early September following observed matings in the laboratory. This abnormally long gestation may be due to delayed implantation, which phenomenon has already been demonstrated in macropods (Sharman 1955).

(*d*) *Litter Size*

All the females examined in the present study had eight teats and the average size of the six litters reared was 6·8, with a maximum of 8 and a minimum of 3. Births all occurred at night and were unfortunately never observed, so that it is not known whether supernumerary juveniles are produced, as in *Didelphis* (Reynolds 1952) and *Dasyurus* (Hill and O'Donoghue 1913). No traces of dead neonatal juveniles were found in the nest-boxes immediately after parturition. The litter which was retained intact and examined at weekly intervals consisted of eight juveniles, of which one disappeared at about 8 days post-partum. Of the remainder, three were males and four females. No valid values for sex ratio can be drawn from the remaining litters since juveniles were detached from the teats and killed for preservation at stages when their sex was indeterminable.

IV. Development of Pouch Young

(*a*) *Description of Neonatus*

At an age of less than 24 hr, a young *A. flavipes* has a crown–rump length of 4·9 mm and weighs 0·0164 g. The integument is completely naked, reddish pink in colour, and covered with a wrinkled, transparent epitrichium. Large circular nostrils are present on either side of the muzzle while the mouth is a large circular orifice. The eyes are discernible as faint pigmented circles beneath the epitrichium. There is no trace of an external ear. The fore limbs are powerful and well developed, the manus bears five digits each with a strong claw. The posterior end of the body is relatively undeveloped and is strongly flexed ventrally. The tail is distinct and about 1 mm long. The hind limbs are poorly differentiated and are represented only by paddle-shaped structures without distinct digits. Minute blood vessels can be discerned in the pes, and these ramify into five

separate branches which pass to the primordia of the future digits. Large blood vessels are evident in various regions of the body, particularly on the head and neck. The general appearance of the neonatal *A. flavipes* is shown in Plate 1, Figure 2.

(*b*) *Eyes*

The eyes, at first just visible as faint pigmented circles, become progressively darker and more clearly defined between the 15th and 20th days. The first traces of a transverse slit appear at about 30 days, while by 35 days the circle has become solid and heavily pigmented. The eyes become larger and darker, and the slit becomes more pronounced until the 50th day when eyelashes can be detected. Further development of the eyes occurs until the 60th day when they are fully formed but still closed. They finally open on about the 62nd day.

(*c*) *Ears*

The first traces of the pinnae are seen in the form of minute papillae on about the 20th day. These papillae develop into a minute pinna with the apex directed ventrally by about the 25th day, while up to 30 days the posterior margin of the pinna is directed anteriorly. Further development and enlargement of the pinna occurs, and by the 35th day the posterior edge has become directed caudally. The external ear becomes larger and thinner, and incipient development of the helix can be detected by the 50th day. At 60 days the pinna is fully formed and bears stiff hairs on its inner surface, but the external auditory orifice is still closed. The ears are fully open by about the 65th day.

(*d*) *Rhinarium and Buccal Cavity*

The rhinarium, which is absent in the neonatus, develops rapidly and is well formed by the 15th day, when it first shows its characteristic brown colour. It is fully formed by about the 35th day. In the early stages, the mouth is in the typical circular form which is fused around the teat. By the 25th day incipient formation of the lips is evident, this development proceeding caudally until by the 50th day the lips are fully formed, the mouth is open, and the teeth are just beginning to erupt. All the teeth have erupted by the 84th day with the exception of the median upper incisors and the posterior molars $M\frac{4}{3-4}$.

(*e*) *Hind Foot*

The minute paddle-shaped hind limb bud (see Section IV (*a*)) continues in its undifferentiated condition until the 10th day when the first traces of true digits appear. The presence of a distinct heel can be detected by the 20th day, while the digits are fully formed by the 25th day, but still lack claws. The latter first appear at an age of about 30 days and have become dark in colour by 50 days. The foot-pads begin to develop at about 55 days and have developed their characteristic striations by about 60 days.

(f) *Pelage and Vibrissae*

The development of hair shows a marked gradient from the anterior towards the posterior end of the animal. The first hairs appear on the head in the supra-orbital region on about the 20th day. This growth has extended posteriorly to the shoulders by about the 25th day. At an age of 30 days, the animal has a naked, reddish pink appearance generally, with stiff agouti hairs on the dorsal surface from the rhinarium to the shoulders. A change in the general colour of the animal now occurs so that by the 35th day it has become bluish pink and the hairs

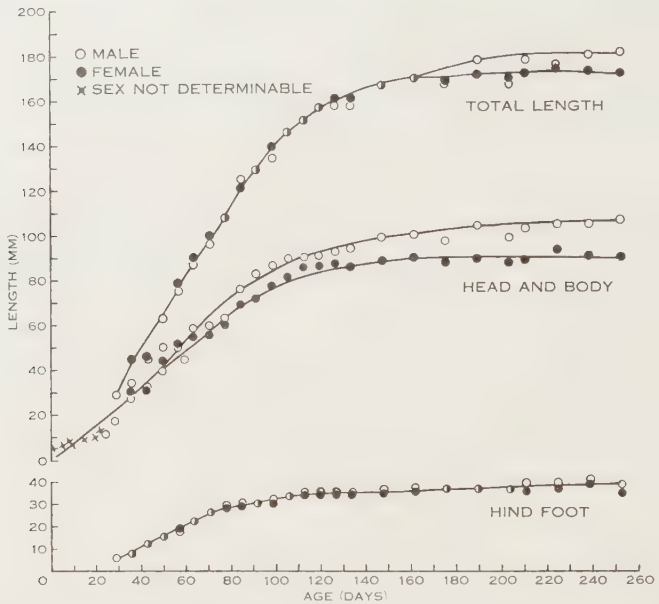

Fig. 1.—Average total length, head and body length, and hind foot length plotted against age in days.

extend to the mid-dorsal region. The belly is still naked. By about 40 days, the main guard hairs extend posteriorly to the sacrum and fine white hairs appear on the external surface of the limbs and on the belly. The darkening of the whole animal continues until, at 50 days, it is completely clothed with fine hairs except for the distal two-thirds of the tail. The animal is furred at about 70 days, with an agouti head and forequarters and grey rump and limbs. The full agouti colour is achieved between 85 and 90 days and at this stage the young *A. flavipes* is fully furred.

The papillae of the mystacial vibrissae first appear at about 15 days, followed by the ulnar-carpal papillae at about 40 days and the genal papillae at 43 days. By 50 days all the vibrissae are present comprising mystacials, genals, supra-orbitals, submentals, inter-ramals, ulnar-carpals, medial antebrachials, and anconeals. Calcaneal vibrissae are not represented in *A. flavipes*. Lyne (1959) has given a detailed account of the vibrissae of marsupials in which he indicates that, although in most species the vibrissae are developed before the pelage hairs, some

exceptions do occur. *A. flavipes* is a case in point, and the late appearance of the vibrissae after the development of the pelage hairs on the head and limbs makes accurate counting difficult. The vibrissal count of *A. flavipes* is: mystacials, rows 1–5, 4, 7, 8, 10, and 9 respectively; genal, 9; supra-orbital, 2; submentals, 6; interramals, 4; ulnar-carpals, 6; medial antebrachial, 1; and anconeal, 1.

(*g*) *External Genitalia*

The external genitalia of the new-born animal is represented by a minute papilla which increases in size gradually and from which protrudes a small peniform structure. At an age of 25 days the small scrotum of the male becomes visible while in the female a slight depression, which contains minute teats, indicates the site of the future pouch area.

Stages of development at 10-day intervals are shown in Plate 2, Figure 1.

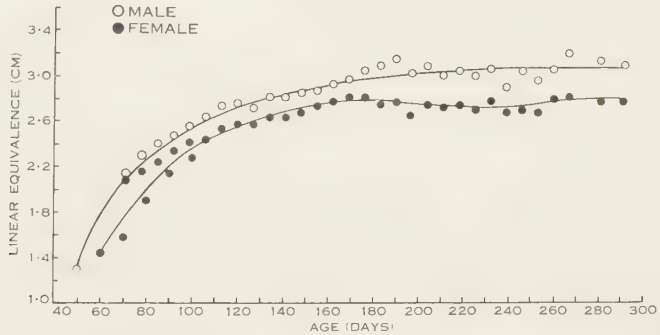

Fig. 2.—Linear equivalence (i.e. cube root of body weight) plotted against age in days.

V. Growth

(*a*) *Choice of Aging Index*

The total length, head and body length, and hind foot length were measured at regular intervals, and the mean of these dimensions were plotted for each sex against the age in days (Fig. 1) to determine which measurements were the most satisfactory aging index. At the same time, the linear equivalence (i.e. the cube root of body weight) was plotted against the age in days (Fig. 2) to make the weights comparable with linear dimensions as described by Lyne and Verhagen (1957). Indications of sexual dimorphism are shown in total length and head and body length, but not in the hind foot length. The curve for total length shows an increase over a longer period of time than do the others. It is thus the most satisfactory aging index, and from it, the age can be calculated with reasonable accuracy up to about 130 days.

(*b*) *Relative Growth*

The total length, head and body length, and hind foot length were also plotted against the linear equivalence as a scatter diagram in which the sexes are recorded separately (Fig. 3). The total length was found to show a more rapid develop-

ment than head and body length and hind foot length. Sexual dimorphism is also shown by this scatter diagram, with the males achieving both larger size and weight than females of comparable age.

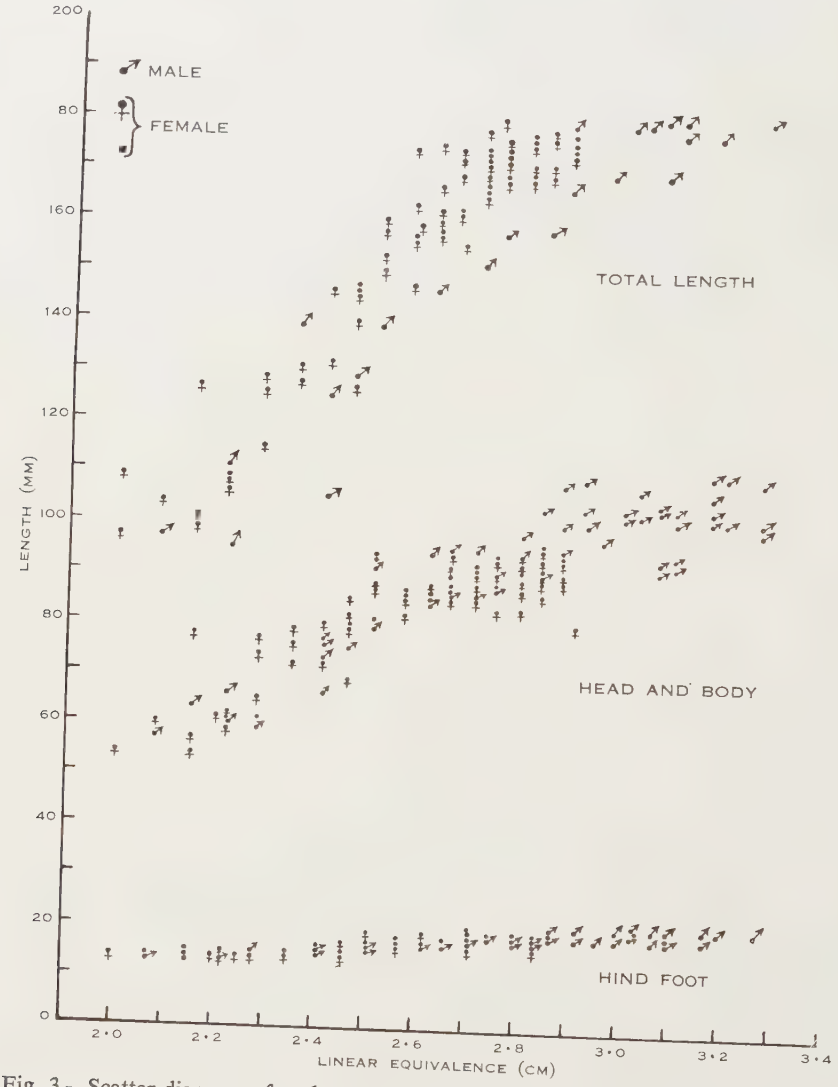

Fig. 3.—Scatter diagram of male and female total lengths, head and body lengths, and hind foot lengths plotted against linear equivalence.

VI. Life History

(*a*) *Pouch Life*

The juveniles of *A. flavipes* are firmly attached to the teats for the first 40 days, but after this time they may move around in the pouch changing from one teat to another. At 70 days they begin to relinquish the teats for longer periods,

during which time they may ride about on the back of the female, retaining their position by gripping the fur with their teeth and fore feet. They finally become fully independent at about 90 days, when they no longer suckle or retain their hold on the female. The degeneration of the pouch in the adult is extremely protracted, and the hypertrophied condition persists for about 35 days after suckling has ceased. Pouch atrophy then commences and continues for a further 30 days by which time the pouch area has returned to its normal inconspicuous condition.

(*b*) *Free-living Juveniles*

Under normal circumstances, young *A. flavipes* of the same litter will live peacefully together in the same cage in the laboratory after the removal of the adult female. Two cases of cannibalism were discovered during the present investigation. On both occasions the animals had been left in a situation where they could not obtain food readily and had attacked and eaten one of their litter mates. In one of these an adult female was housed with her litter of three, two young females and a young male. The frozen mouse carcases which had been provided as food for this group during a week-end had become badly decomposed during very hot weather, and it is presumed that the three females attacked and ate the young male, whose sole remains consisted of the anterior portion of the skull. No second generation was reared during this present study, but courtship behaviour was observed between litter mates reared in captivity at an age of about 320 days. This may indicate that sexual maturity is achieved at this time and that the young animals mate in the August of the year which follows their birth. The major features in the life history and development of *A. flavipes* are shown in Table 1. These can be used in conjunction with the graph of total length *v.* age to assess the age of specimens from birth to about 140 days.

VII. Discussion

(*a*) *Comparison with other Marsupials*

A. flavipes has the smallest neonatus so far investigated, its crown–rump length measuring only 4·9 mm and its weight 16·4 mg. *Dasyurus quoll* is larger at birth, its crown–rump length measuring 7 mm, yet it is lighter, weighing only 12·5 mg (Hill and Hill 1955). In spite of this, *A. flavipes* has a remarkably long gestation period, which is exceeded only by some of the macropods such as *Macropus major* with a period of 39 days (Owen 1834). *A. flavipes* has a rate of development comparable with that of *Didelphis virginiana*, in which the eyes open between 58 and 72 days and the young become free-living at about 100 days (Reynolds 1952). Development in this marsupial mouse is appreciably slower than in the long-nosed bandicoot, *Perameles nasuta*, which has the most rapid development of any marsupial so far investigated, since the eyes open between 45 and 48 days and the animal is free-living by 70 days (Lyne, unpublished data). A comparison of birth weights and measurements of marsupials is given in Table 2. The neonatus of *A. flavipes* is compared with that of *Trichosurus vulpecula* in Plate 2, Figure 2.

TABLE 1

DEVELOPMENT AND LIFE HISTORY OF ANTECHINUS FLAVIPES

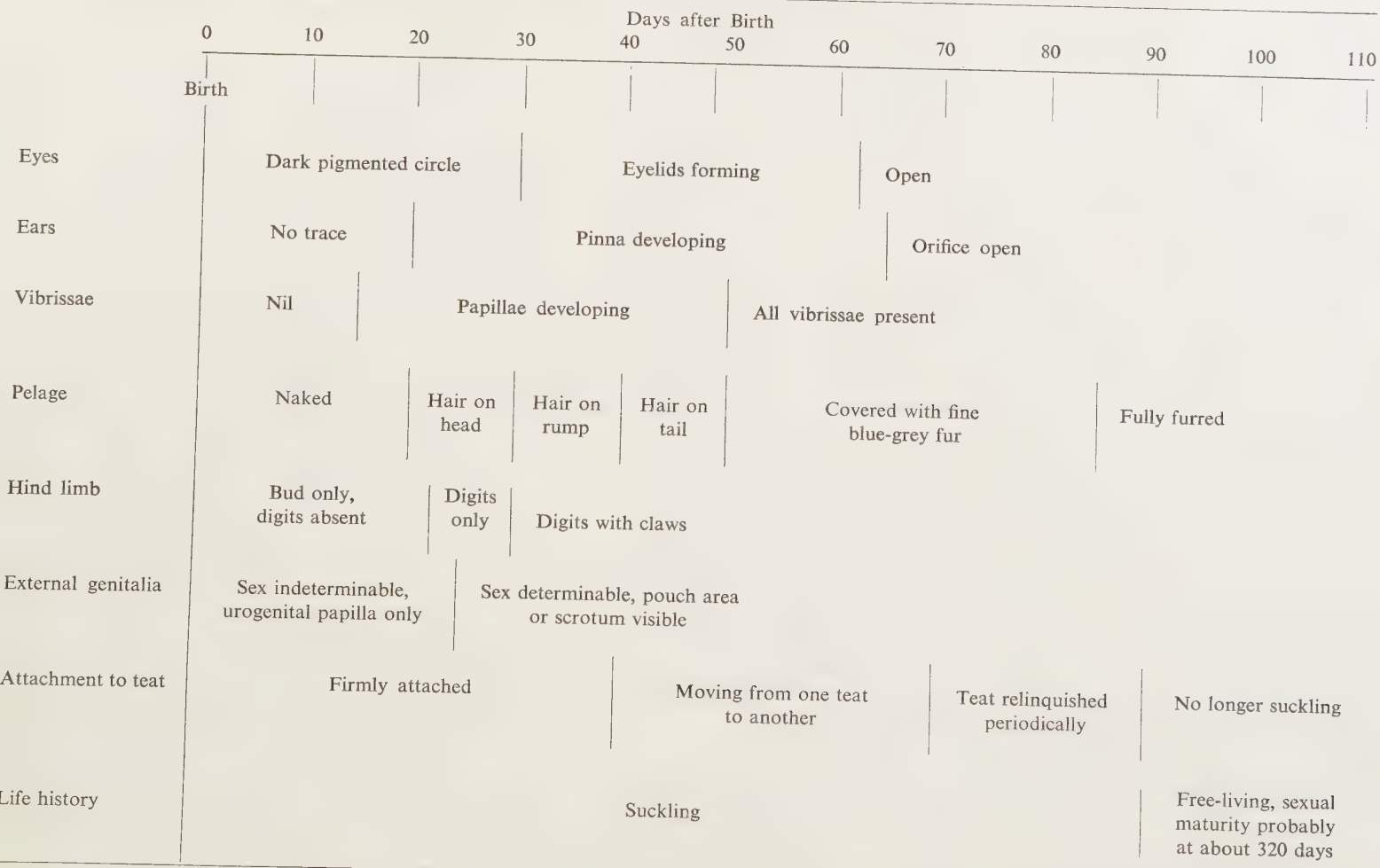

TABLE 2

COMPARISON OF LIFE HISTORY AND DIMENSIONS OF ANTECHINUS FLAVIPES WITH OTHER MARSUPIALS

Species	(A) Gestation Period (days)	(B) Birth Weight (g)	(C) Birth Crown–Rump Length (mm)	(D) Eyes Open at Day:	(E) Free-living at Day:	(F) Mean Litter Size	(G) Mean Weight (g) of Adult ♀	References	
Antechinus flavipes	31·5	0·0164	4·9	62	90	6·8	31		
Dasyurus quoll	8–16	0·0125	7	80	126	6	600	A	Hill and O'Donoghue (1913)
								B, C, F	Hill and Hill (1955)
								D, E	Fleay (1935)
								G	Marlow, unpublished data
Didelphis virginiana	13	0·1617	11·5–13·8	58–72	96–108	7·2	1350	A, C, D, E, F	Reynolds (1952)
								B, G	Hartman (1952)
Perameles nasuta	11+	0·20	13	45–50	70	2·4	860	A–G	Lyne, unpublished data
Trichosurus vulpecula	17·5	0·20	13	87·5–122·5	150–178	1	2030	A, B, C, G	Lyne, Pilton, and Sharman (1959)
								E, F	Dunnet (1956)
								D	Lyne and Verhagen (1957)
Setonix brachyurus	27	0·45	30	105	260–280	1	3120	A	Sharman (1955)
								D	Sharman (1957)
								B, C, E, F, G	Waring *et al.* (1955)

(*b*) *Comparison with Eutheria*

The contrast in dimensions of the neonatus and life history of *A. flavipes* and a placental of comparable adult dimensions such as *Mus musculus* is remarkable. The gestation period of the marsupial exceeds that of the placental by 10 days, while the lactation period is about 70 days longer. The new-born placental is appreciably larger and heavier than its marsupial counterpart, its crown–rump length measuring 28 mm and its weight 1·3 g (Gruneberg 1952). The general rate of development of the placental far exceeds that of the marsupial, the eyes of *Mus musculus* opening at 14 days, and sexual maturity being achieved in 40 days.

(*c*) *Ratio of Body Weight of Neonatus and Adult Female*

Comparisons of the neonatal weight *v.* adult female weight between marsupials and placentals have been made by Hartman (1952) and Leitch, Hytten, and Billewicz (1959). The latter authors stress the need to consider the weight of the whole litter rather than that of an individual juvenile, and they express the ratio as (litter weight/maternal weight) × 100. This value for *A. flavipes* is 0·4%, while the ratio of the weight of a single neonatus/weight of adult female is 1/2000 and for a litter of eight is 1/250. Hartman (1952) indicates that the greatest disparity between the weight of juvenile and adult female exists in the larger kangaroos where the ratio is 1/60,000.

(*d*) *Conclusion*

Much work still remains to be done to further our knowledge of the reproduction of marsupials, particularly the Dasyuridae. Further investigation of the very long gestation period of *A. flavipes* is needed, together with comparative studies on the pattern of reproduction in other marsupial mice such as *Sminthopsis* spp. and *Planigale* spp.

Many advantages would be obtained from the establishment of a polytochous marsupial as a laboratory animal, but at present there is little to recommend *A. flavipes* in this role owing to its restricted reproductive pattern and the difficulty of handling it in the laboratory. It is possible that its reproductive rate might be increased by artificial illumination and by the injection of hormones.

VIII. Acknowledgments

The author wishes to express his gratitude to Dr. A. G. Lyne, Division of Animal Physiology, C.S.I.R.O., for his helpful suggestions in the preparation of this paper and for the loan of the specimen of *Trichosurus vulpecula* shown in Plate 2, Figure 2; to Mr. F. N. Ratcliffe, Division of Entomology, C.S.I.R.O., and Mr. J. Calaby, Wildlife Survey Section, C.S.I.R.O., who read the manuscript and offered helpful advice; and also to Miss B. Kindred, Division of Animal Genetics, C.S.I.R.O., for supplying surplus mice on which the colony of *A. flavipes* was fed. Finally, the author would like to thank Mr. H. Hughes, Australian Museum, Sydney, for the photography.

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Explanation of Plates 1 and 2

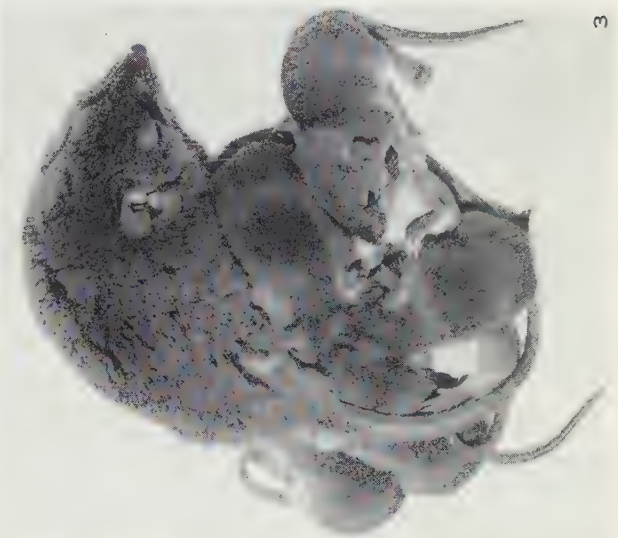
Plate 1

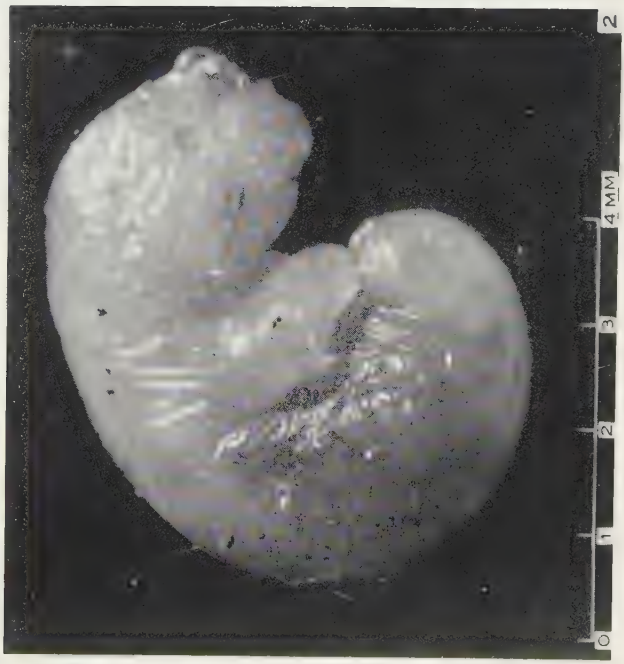
Fig. 1.—Adult female *A. flavipes.*
Fig. 2.—Neonatus *A. flavipes.*
Fig. 3.—Adult female *A. flavipes* and litter 68 days old.

Plate 2

Fig. 1.—Pouch young of *A. flavipes* at 10-day intervals from 10 to 60 days of age.
Fig. 2.—Comparison of neonatus *Trichosurus vulpecula* (left) and *A. flavipes.*

REPRODUCTION OF ANTECHINUS FLAVIPES





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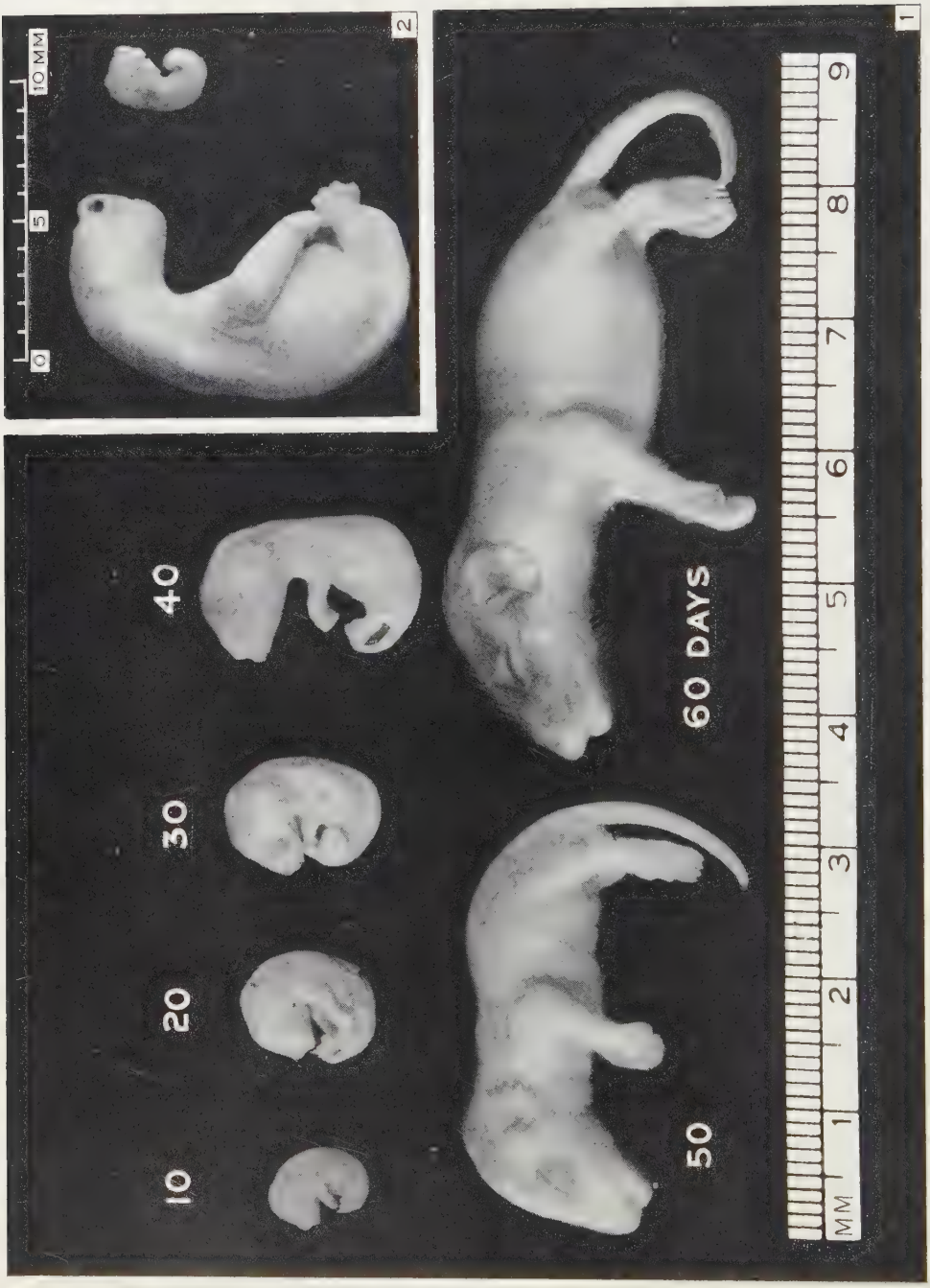

FUNCTIONAL MORPHOLOGY, MICRO-ANATOMY, AND HISTOLOGY OF THE "SYDNEY COCKLE", *ANADARA TRAPEZIA* (DESHAYES) (LAMELLIBRANCHIA: ARCIDAE)

By G. E. Sullivan*

[*Manuscript received November* 14, 1960]

Summary

The anatomy and histology of the Australian lamellibranch, *Anadara trapezia* (Deshayes, 1839), are described.

The pattern of the ciliary currents on the ctenidia, mantle, foot, and labial palps is similar to those in the related species *Arca tetragona* and *Glycymeris glycymeris*. However, *A. trapezia* differs from these forms in having a more extensive development of the ridges on the labial palps, as well as in the ciliation of the ctenidial filaments. The possible correlation between the arrangement of cilia on the ctenidial filaments and the extent of the ridged areas of the palps is discussed.

The structure of the stomach is closely similar to that of *Glycymeris*. The digestive diverticula, with their ciliated ducts, are typical of the Anisomyaria and Eulamellibranchia.

The gastric shield appears to be secreted by the epithelial cells of the stomach. Secretion is intermittent, resulting in stratification of the shield, and is indicated by strongly periodic acid–Schiff(P.A.S.)-positive material which forms in the neighbourhood of the epithelial cell nuclei and then migrates to the apical ends of the cells to be added to the shield.

Many gland cells, both intra-epithelial and subepithelial, are present in the foot, mantle, and palps. There are several types, differing in their staining reactions and in the appearance of their cytoplasm in fixed and sectioned material. It is suggested that those glands whose cytoplasm gives a very strong positive reaction with P.A.S. may produce a lubricating secretion, while those which give reactions for mucin but are not so strongly P.A.S.-positive may form a tacky mucus suitable for holding particulate matter to facilitate transport by ciliary currents.

In the connective tissue there are stellate cells embedded in the gelatinous ground substance. Another type of cell, laden with coarse brownish granules is present in some regions, especially around the kidney tubules. "Leydig's cells", which have been observed in the connective tissue of a number of molluscs, and which store glycogen in these forms, do not appear to be present in *A. trapezia*. Glycogen is present, but is scattered through the ground substance in the form of granules. It is suggested that the glycogen may be deposited in the fine processes of the stellate cells.

I. Introduction

This paper presents the results of an investigation of the anatomy and histology of one species of lamellibranch, *Anadara trapezia* (Deshayes, 1839), and is intended as a starting point for comparative studies in the physiological histology of molluscs.

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A. trapezia was selected for several reasons. It is one of the small number of lamellibranchs with red blood and is of interest on this account. A more detailed study of its blood cells is planned as the subject of a subsequent investigation. The ready accessibility of its habitat facilitates field observations and allows the easy collection of specimens. It is extremely abundant, a circumstance which, together with the ease with which it can be studied in its habitat, should facilitate any ecological or population studies which might be undertaken at a later date.

Lamellibranchs of the family Arcidae have the following features: the hinge-line of the shell is elongated and straight and is provided with numerous teeth (taxodont dentition); both adductor muscles are present (dimyarian condition) and are either of equal size or with the anterior one quite large even in those species where it is reduced; the ctenidia are of the filibranch type; the blood is red in colour, and the pigment is carried in nucleated erythrocytes. In all these respects, *A. trapezia* is a typical member of the family.

A. trapezia is found on estuarine mudflats along the Australian coastline. The specimens used in the present study were collected at Gunnamatta Bay, near Sydney. Gunnamatta Bay is a large inlet of the sea, and is very shallow except for a deep and narrow channel along one side. It is sheltered by land, and the ocean swell does not reach it, so that there is no surf. At low tide, a sandy mudflat several hundred yards across is exposed. The mudflat consists of slightly raised areas alternating with extensive shallow pools about a foot deep. The pools contain plants, *Zostera* and *Posidonia* being particularly abundant. Among the plants, and buried in the substrate, there is a rich and varied fauna. A number of species of lamellibranchs is present, including *A. trapezia*. In the pools, the animals of the latter species lie partly buried in the substrate, with only the posterior ends exposed. They are abundant, often several dozen to the square foot, frequently so closely packed that they occupy most of the surface area. Fronds of seaweed, often several inches long, may be found attached to the posterior end of the shell but absent from the remainder of it, an indication that the animal is not a deep burrower, but normally lives obliquely orientated in the substrate with its anterior two-thirds or thereabouts buried and the posterior region exposed to permit access of water to the mantle cavity.

The living habits resemble those of the European cockle *Cardium*, and the shell is similar in appearance to that of the cockle, hence the term "Sydney cockle" which is frequently found in the literature (e.g. Iredale 1939; Dakin, Bennett, and Pope 1952). According to Johnstone (1899), *Cardium edule* "is gregarious all along the coast line where suitable bottoms exist, but the great cockling beds are, as a rule, found only in sheltered waters, in shallow bays, and at the mouths of estuaries . . . The cockle inhabits the topmost layer of the sand, burying itself to the depth of an inch at most. It lies in an oblique position . . . In some places the cockles commonly bear a tuft of algae, and the position of the animal in the sand can be determined by the presence of this projecting tuft". These remarks apply almost equally well to *A. trapezia*.

A parasitic acanthocephalan worm was frequently encountered in dissections. It was often found in such places as the posterior adductor and posterior foot retractor muscles. The incidence of parasitism by this worm appears to be high.

II. Methods

Several fixatives were employed, satisfactory results being obtained with Bouin, Zenker, and Susa. After washing, pieces of tissue were dehydrated in graded ethanols, cleared in cedar-wood oil, washed free of the oil in xylene, and embedded in paraffin. Sections 4–10 μ thick were cut for histological study. For general staining, Ehrlich's haematoxylin counterstained with phloxine was employed. Azan was used to stain connective tissue fibres; it is also useful as a general stain. Other stains used were: Heidenhain's iron haematoxylin alone or in combination; thionin and Mayer's mucicarmine for the identification of certain mucous glands; Gomori's aldehyde–fuchsin, an excellent means of showing ducts of glands, which other methods often failed to show. The periodic acid-Schiff (P.A.S.) reaction was used in the study of gland cells, and for demonstrating glycogen in sections compared with saliva-treated controls.

Live animals were dissected in sea-water and the principal ciliary currents were identified with the aid of carmine particles.

The anatomy was studied in dissections, as well as in sections 10 μ thick cut through a whole animal which had been fixed in Bouin and embedded in paraffin. The alimentary system was studied in reconstruction from serial sections as well as by means of rubber casts made by injecting "Neoprene" latex into the mouth with a syringe and subsequently removing the surrounding tissues by maceration in concentrated hydrochloric acid; in addition the stomach was opened in live specimens and the ciliary currents in it were observed.

III. Observations

(*a*) *General Body Form*

The soft parts are enclosed in a stout equivalve and inequilateral shell. The hinge-line of the shell is long and straight, with numerous teeth; in this respect the shell is different from that of the true cockle. In general appearance the shell resembles that of *Cardium*. Its external surface is sculptured by about 30 prominent ridges radiating from the umbo to the periphery, and is covered by a horny brown periostracum which is most abundant towards the periphery, having been worn away on the older parts of the shell. Towards the periphery the inner surface of each valve is excavated by radial grooves corresponding in position to the external ridges. The grooves are occupied in life by muscular thickenings of the mantle border (Fig. 1,*A*).* Similar grooves are present in the shell of *Cardium* (Johnstone 1899, fig. 10).

The animal is bilaterally symmetrical, but there is some internal asymmetry, in the vascular and alimentary systems (Fig. 1,*C*,*D*). The two sheets of tissue forming the mantle are completely separated ventrally; although the mode of life resembles that of *Cardium*, siphons are not present. The anterior adductor muscle is somewhat reduced. The suspensory membrane supporting the ctenidial filaments is produced posteriorly into a pointed flexible tip. The anterior portions of the

* Abbreviations used in Figures 1–13 are explained in Appendix I.

ctenidia extend up into the umbonal regions, whence the elongated labial palps pass ventralwards to the mouth. There is a large protrusible foot with a deep ventral groove. The ducts of subepithelial gland cells open into the groove, and on to the ventrolateral surfaces in the neighbourhood of the groove (Fig. 6).

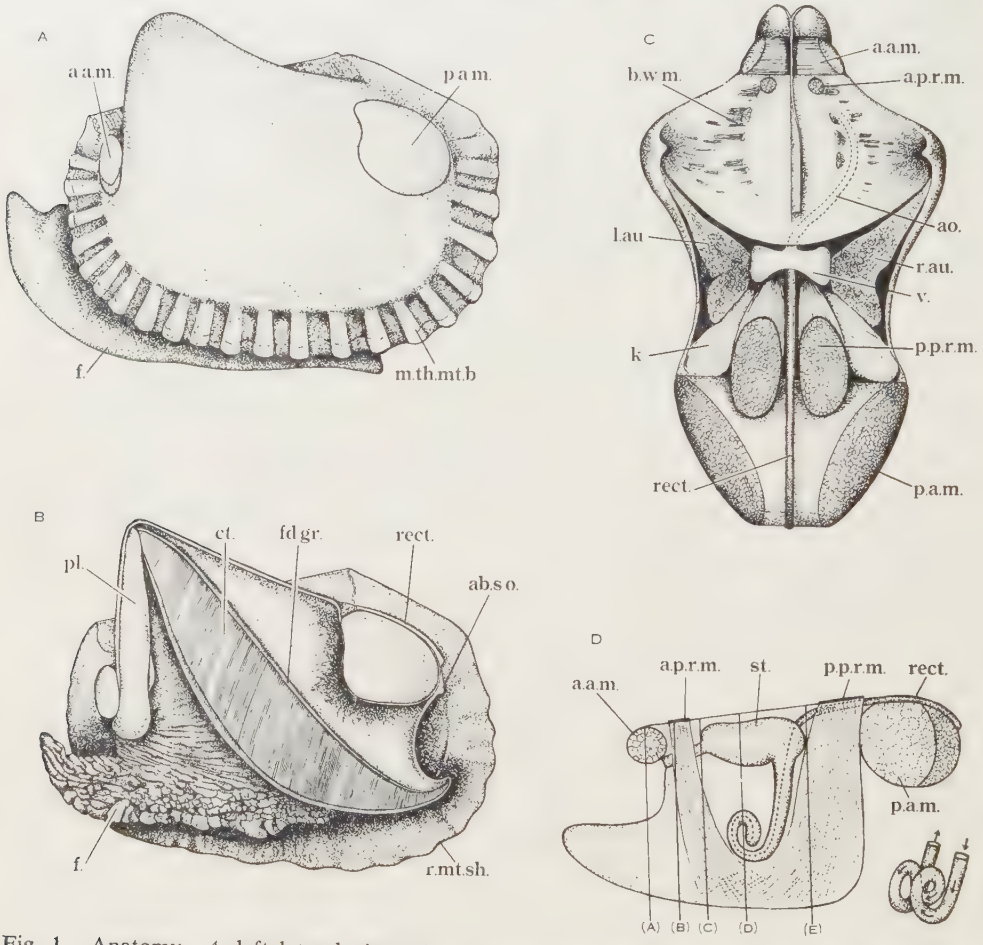

Fig. 1.—Anatomy. *A*, left lateral view of the animal, with the foot extended. *B*, left lateral view of the organs in the mantle cavity, exposed by removal of the left mantle sheet. The foot is partially retracted. *C*, dorsal view of a dissection to expose the heart and kidneys. The aorta is indicated by dotted lines. *D*, diagram of the alimentary canal. The loops of the intestine are shown at lower right; the arrows indicate the flow of the contents. The lines (*A*)–(*E*) indicate the levels of the transverse sections in Figure 2.

The ventral portion of the foot is pigmented, the pigment being confined to the epithelial cells; pigment is also present in the epithelium of the mantle border (Fig. 5,*A*). The pigmentation of the mantle border is most marked in the posterior region, the pigment having presumably been deposited in response to illumination. It has long been known that pigment granules are formed in lamellibranchs under the influence of light (List 1899).

Whitish patches are present in the posterior part of the mantle border, in the free tips of the suspensory membranes of the ctenidia, and in neighbouring tissues. Atkins (1936) observed similar markings in *Glycymeris glycymeris*, and she commented that they were formed in those regions likely to be reached by light. The nature of the whitish spots in *A. trapezia* is discusssed in Section III(*l*).

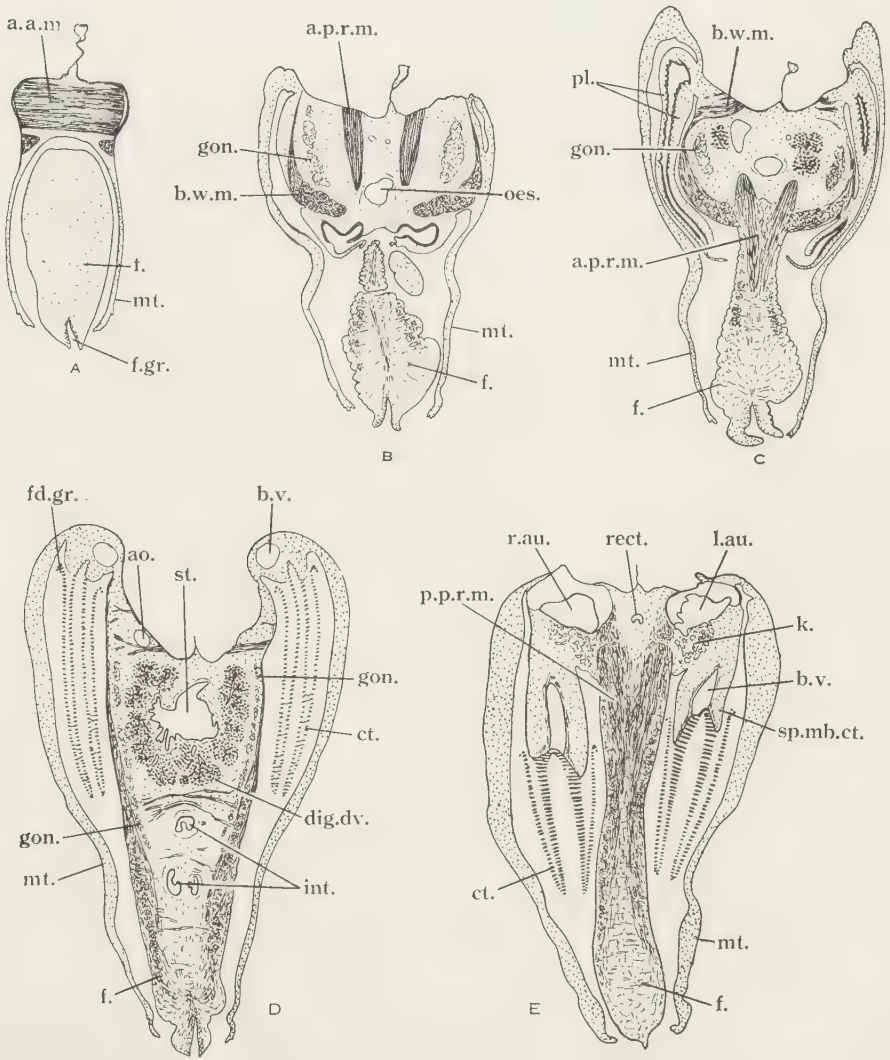

Fig. 2.—Transverse sections through the animal at the levels of (*A*)–(*E*) in Figure 1.

(*b*) *The Mantle* (*Pallium*)

(i) *Terminology.*—The foot, ctenidia, and labial palps are contained in the mantle cavity which is enclosed by two large flat sheets of tissue (the mantle), attached to the inner surfaces of the shell valves. The outline of each sheet is

approximately semicircular. Each sheet is fastened to the shell by an elongated linear attachment running parallel to the edge of the valve. This attachment is the pallial or mantle attachment; its position on the inner surface of the shell is indicated by the pallial line.

A portion of each mantle sheet is situated peripheral to the pallial line. In textbooks this is often called "mantle edge" (e.g. Morton 1958, fig. 21,*A*);

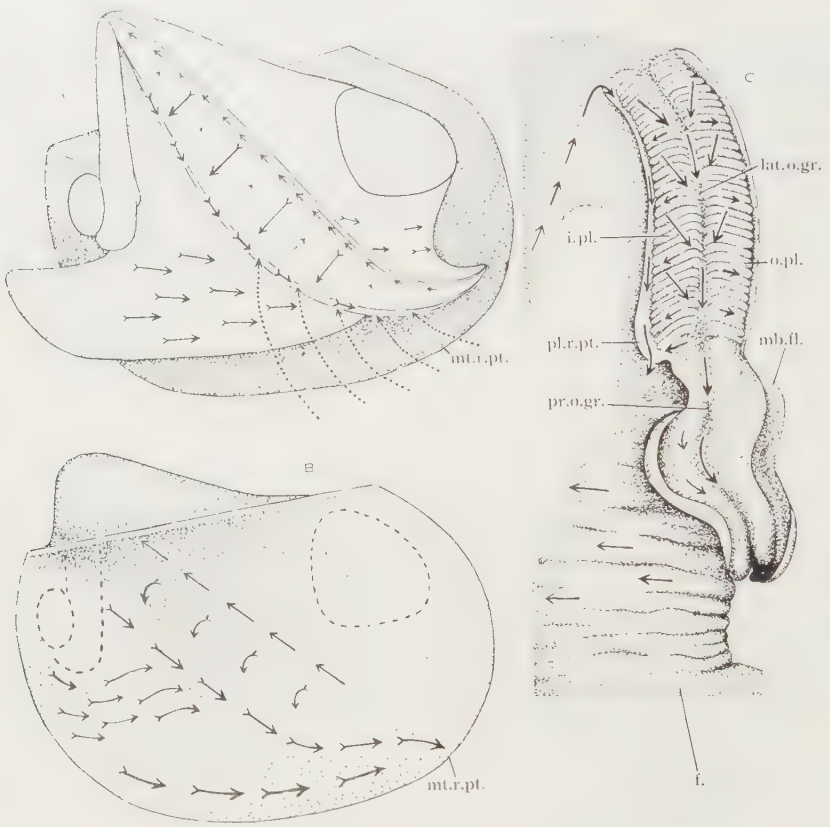

Fig. 3.—Ciliary currents in the mantle cavity and on the labial palps. In *A* and *B*, the tail-less arrows indicate feeding currents, the tailed arrows, rejection currents. In *A*, dotted arrows show the inhalant water current.

however, since this part of the mantle is an elongated flattened strip of tissue, the terms "mantle margin" or "mantle border" are more suitable, the term "edge" being restricted to the most peripheral portion of the border where there is a transition from the lateral to the medial surface. In lamellibranchs the mantle border carries three folds; they are not very marked in *A. trapezia*. In the literature there is some ambiguity, for the term "lobe" has been used for these folds, and also for each sheet of the mantle. In this paper, I propose to use the term "mantle border" for the free portion peripheral to the pallial line and the word "edge"

will refer only to the most peripheral portion of the border. The word "fold" will be used for each of the three differentiated regions of the border (Fig. 4). The portion of the sheet central ("dorsal") to the mantle line will be referred to as the "central portion" of the mantle. The surface of the sheet facing the mantle cavity may be called "medial" or "inner" surface, while the lateral surface which faces the shell may be called "outer" or "lateral" surface.

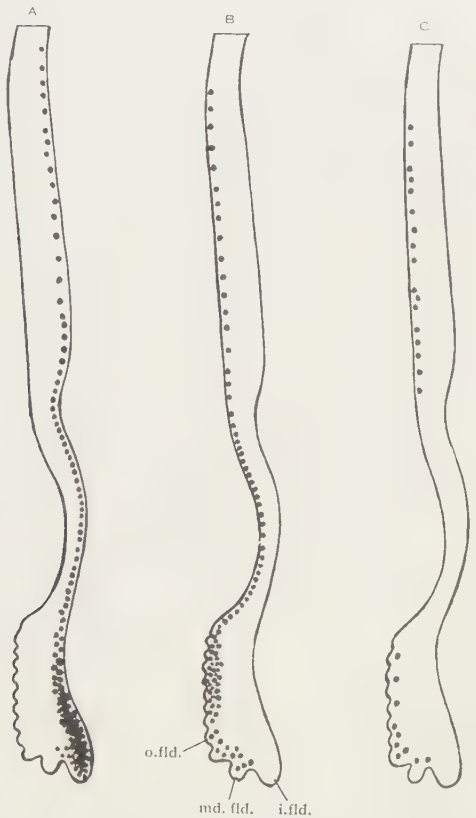

Fig. 4.—Distribution of gland cells as seen in a transverse section of the mantle border. *A*, type *MA*; *B*, type *MB*; *C*, type *MC*.

(ii) *General Description.*—The extensive central portion of each mantle sheet consists mainly of gelatinous connective tissue containing large blood spaces which form a capacious reservoir. When a fresh animal is opened, the central portion of the sheet usually appears engorged with blood and dark red in colour: if it is punctured there is considerable loss of blood.

In the mantle border, muscle fibres are abundant, making possible the retraction of the border when it is irritated.

(iii) *Musculature.*—Practically all of the muscle in the mantle is restricted to the border. Most of the fibres are radial, taking origin from the pallial line via

a specially modified portion of the epithelium. They are mostly concentrated into about 22 thickenings (Fig. 1,*A*) which occupy the grooves on the inner surface of the shell. There is in addition a well-developed circumferential musculature, consisting of fibres arranged parallel to the edge. There are also some scattered transverse fibres.

Below the medial epithelium of the border, the radial and circumferential fibres are arranged in three distinct layers (Fig. 5,*C*). The thinnest layer, which lies closest to the surface, and the deepest layer, which is the thickest of the three, consist of radial fibres, while the middle layer consists of circumferential fibres.

(iv) *Gland Cells.*—Both intra-epithelial and subepithelial glands are present. In the central portion the gland cells are mainly intra-epithelial and are numerous, not only in the epithelium of the surface facing the mantle cavity, but also in that next to the shell. Those in the lateral epithelium contain large spherical droplets

TABLE 1

STAINING REACTIONS OF GLAND CELLS IN THE MANTLE BORDER*

Stain	Type *MA*	Type *MB*	Type *MC*
Iron haematoxylin and phloxine	Pale brick red	Brick red	Black or red
Iron haematoxylin and mucicarmine	Pink	Pink	Black
Mucicarmine alone	Pink	Pink	Colourless
Ehrlich's haematoxylin and phloxine	Pale mauve	Mauve	Bright pink
Thionin (examined in water)	Pink (metachromatic)	Pink (metachromatic)	Colourless
Periodic acid–Schiff	Pale pink	Deep magenta	Deep magenta
Azan	Pale blue	Blue	Red or blue
Gomori's aldehyde–fuchsin	Purple	Purple	Colourless

* See also Figures 4 and 5, pp. 225, 227.

which sometimes stain black with iron haematoxylin and sometimes remain unstained; with azan, some of the glands stain red, others blue; all give a strong P.A.S. reaction. It is uncertain whether the different staining reactions to azan and to iron haematoxylin reflect stages in the secretion cycle of a single type or indicate two different types of gland cell.

Gland cells are very numerous in the border, especially in its most peripheral region close to the edge. They are subepithelial, and there are three types which may be distinguished by their staining reactions and the appearance of the cytoplasm. They will be designated by the letters *MA*, *MB*, and *MC*, the letter *M* indicating that they belong to the mantle. The distribution of the three kinds is shown in Figure 4 and their staining reactions are listed in Table 1.

Type *MA* (Fig. 4,*A*) has a very vacuolated cytoplasm (Fig. 5,*C*). These cells are abundant in the inner fold of the border, where they lie among the muscle fibres. The contraction of the muscle fibres, in addition to effecting movements of the border, possibly assists in the expulsion of the secretion.

Type *MB* (Fig. 4,*B*) differs from type *MA* in having a non-vacuolated, coarsely granular cytoplasm. It gives a strongly positive P.A.S. reaction, compared with *MA*, which gives a much less intense coloration.

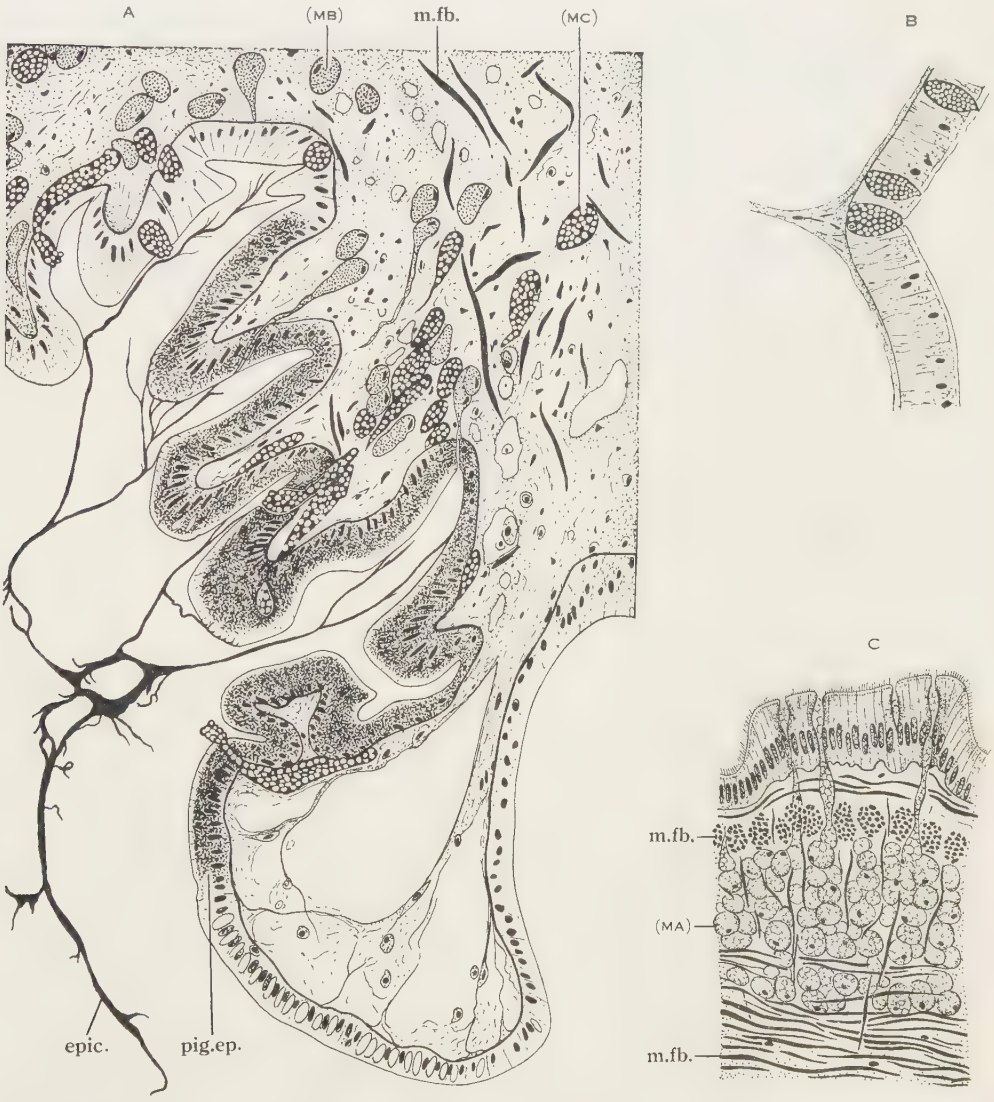

Fig. 5.—Histology of the mantle. *A*, portion of the mantle border showing the epithelium which secretes the epicuticle, the *MB* and *MC* gland cells, and pigment granules in much of the epithelium; *B*, the outer epithelium of the central portion; *C*, portion of the border showing the ciliated inner epithelium, the *MA* glands, and the muscle fibres arranged in three layers.

Both types *MA* and *MB* stain pink with Mayer's mucicarmine and metachromatically with thionin; they are therefore to be regarded as mucous glands.

Type *MC*, which is subepithelial (Fig. 4,*C*) remains colourless with mucicarmine and thionin. It is strongly P.A.S.-positive and the large droplets

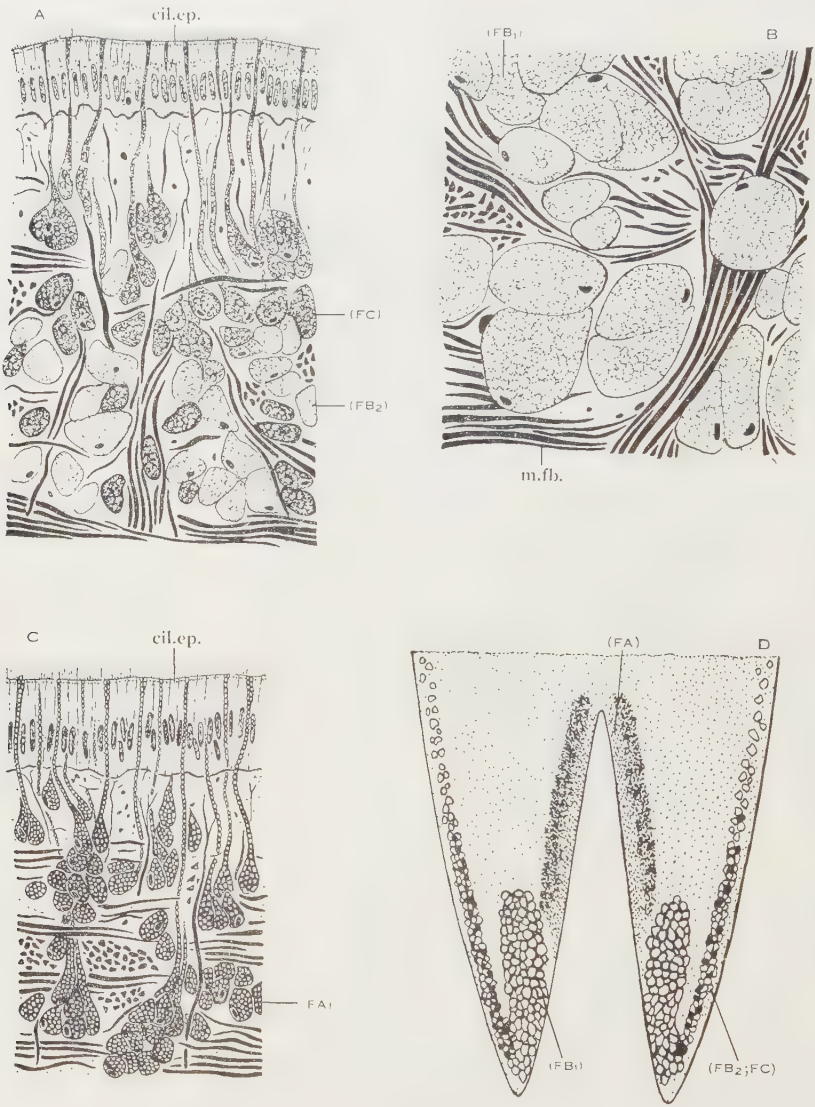

Fig. 6.—Histology of the foot. *A*, the FB_2 and *FC* gland cells; *B*, the large FB_1 gland cells; *C*, the *FA* gland cells (*A*, *B*, and *C* all to the same scale). *D*: distribution of the gland cells as seen in a transverse section of the foot.

stain black with iron haematoxylin. It resembles, if it is not in fact identical with, the type of intra-epithelial gland cell in the lateral epithelium of the central portion of the mantle sheet.

(v) *Epithelia.*—The epithelium facing the mantle cavity is ciliated (Fig. 5,*C*) and contains many unicellular glands. In the border, the apical cytoplasm of the epithelial cells is laden with dark brown pigment granules (Fig. 5,*A*). The epicuticle or periostracum is formed by the epithelial cells in the region of transition between the inner and outer folds (Fig. 5,*A*).

The epithelium on the outer surface of the mantle is not ciliated. At the level of the pallial line the cells are specially modified to form a firm union with the shell and to provide an origin for the radial muscle fibres of the border. The epithelium at this level consists of low cells whose cytoplasm contains many fine fibres passing from the base to the apical end.

The outer epithelium of the central portion consists of cells whose cytoplasm is traversed by numerous fine fibrils (Fig. 5,*B*). The compact, darkly staining nuclei lie in the apical ends of the cells; a similar feature was observed in *Anodonta* by Siebert (1913).

TABLE 2

STAINING REACTIONS OF GLAND CELLS IN THE FOOT*

Stain	Type *FA*	Types FB_1 FB_2	Type *FC*
Iron haematoxylin and mucicarmine	Black	Pink	Pink
Mucicarmine alone	Colourless	Pink	Pink
Thionin (examined in water)	Colourless	Deep pink (metachromatic)	Deep pink (metachromatic)
Ehrlich's haematoxylin and phloxine	Pale brick red	Mauve	Mauve
Periodic acid–Schiff and Ehrlich's haematoxylin	Pale pink	Pale pink	Deep magenta
Gomori's aldehyde–fuchsin and orange G	Brown	Purple	Purple
Azan	Red	Pale blue	Blue

* See also Figure 6, p. 228.

(*c*) *The Foot*

The foot is a shallow burrowing organ provided with a complex musculature, including two pairs of pedal retractors. It is covered by a ciliated columnar epithelium. Ventrally, many of the epithelial cells contain pigment granules in the apical cytoplasm.

Large numbers of subepithelial gland cells are present in the neighbourhood of the ventral groove. There are three types, differing in their appearance and staining reactions. They will be designated by the letters *FA*, *FB*, and *FC*, the letter *F* indicating that they belong to the foot. Their distribution is shown diagramatically in Figure 6,*D*, and their staining reactions are listed in Table 2.

Type *FA*, discharging into the deeper part of the groove, contains large spherical droplets which stain black with iron haematoxylin and red with azan, but do not react with Mayer's mucicarmine or thionin. Types *FB* and *FC* stain blue with azan, pink with mucicarmine, and metachromatically with thionin.

The *FB* glands include large cells (type FB_1) discharging into the groove, and somewhat smaller ones (type FB_2) whose ducts open on to the lateral surfaces of the foot. Their cytoplasm is greatly vacuolated (Fig. 6,*A*,*C*).

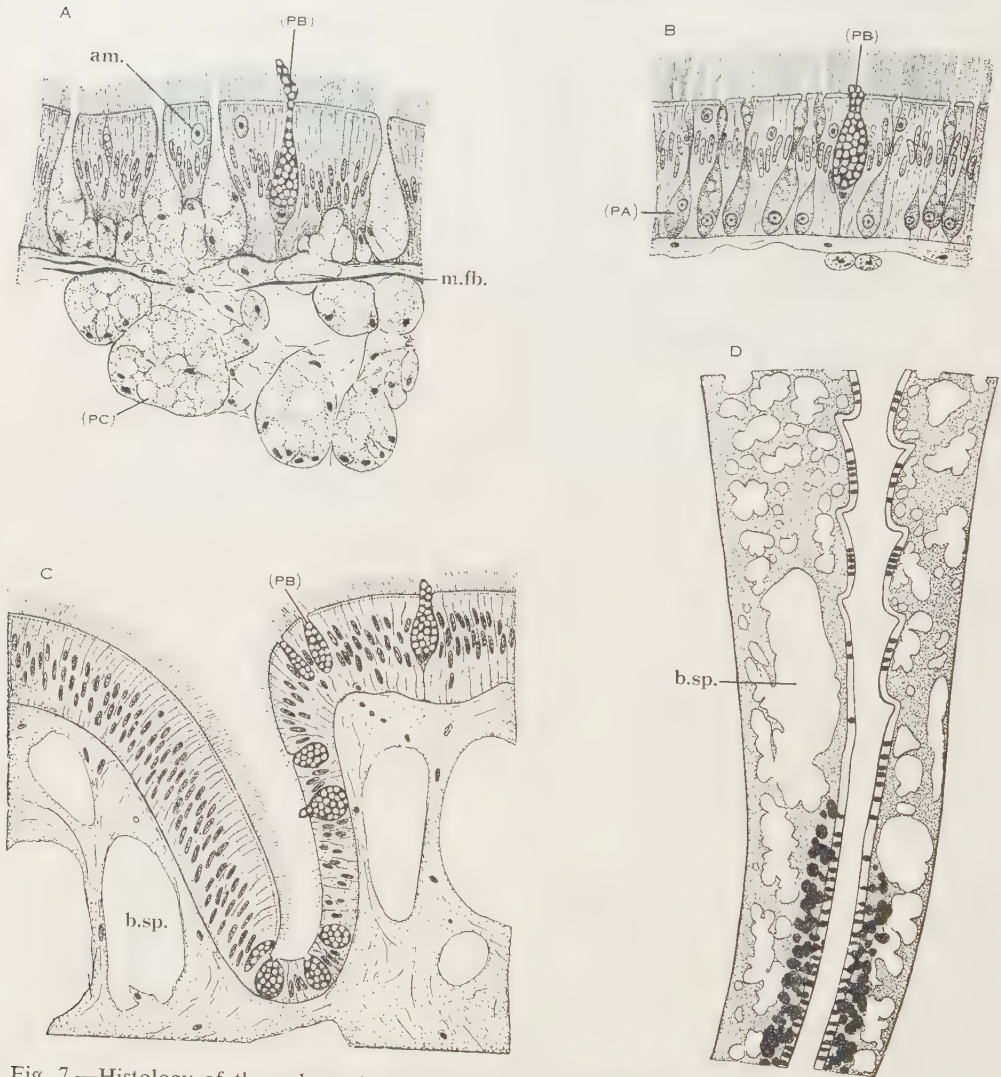

Fig. 7.—Histology of the palps. *A*, part of the smooth portion, showing the *PC* gland cells, some of which are intra-epithelial while most are subepithelial; *B*, epithelium of the smooth portion approaching the mouth, showing the tall cilia and the *PA* gland cells; *C*, section through a groove in the ridged area. The *PB* gland cells are numerous in the dorsal wall of the groove; *D*, low power projection drawing of palps. There are numerous blood spaces in the connective tissue. The *PC* gland cells are shown in solid black; they are entirely intra-epithelial in the ridges but mainly subepithelial in the smooth portions.

The *FC* glands are intermingled with type FB_2. They secrete on to the lateral surfaces of the foot. With some of the stains used they are barely distinguishable

from the FB_2 cells, but they give a stronger P.A.S. reaction and stain a deeper blue with azan than do the latter. Their cytoplasm does not seem to be as vacuolated as that of the FB_2 cells. It is uncertain whether the FB_2 and FC cells are different stages in the physiological activity of a single type, or whether they are two kinds differing in the composition of their secretion; the latter alternative seems the more likely (see Section IV).

(*d*) *The Labial Palps*

There are two pairs of elongated labial palps, one pair on each side, extending from the anterior ends of the ctenidia to the mouth (Fig. 1,*B*; Fig. 2,*C*). The inner surfaces of each pair face each other. In Figure 3,*C*, the lateral (outer) palp has been reflected to expose the medial (inner) palp.

Each palp consists of a dorsal portion, bearing about three dozen transverse ridges, and a ventral smooth portion between the ridged area and the mouth (Fig. 3,*C*). The free posterior border of the inner palp is slightly expanded at the level of the ventral end of the ridged portion to form a rejection point at which material is cast off to be carried away by ciliary currents on the foot. The free border of the smooth portion of the outer palp is greatly expanded into a thin membranous flap which fits over the free edge of the smooth portion of the inner palp, thus making of the smooth portions of the palps an enclosed tube in which food material is transported to the mouth. In this manner the flap probably serves to prevent loss of food from the proximal oral groove.

The oral groove extends from the dorsal extremity of the palps to the mouth. The term was introduced by Kellogg (1915), who named the portion between the ridged areas, "lateral oral groove", and that passing between the smooth portions of the palp, "proximal oral groove". After sorting of food from other material has taken place on the ridged areas, the food particles are conveyed down the oral groove to the mouth.

The palps consist mainly of gelatinous connective tissue containing many blood spaces. A few muscle fibres, concentrated mainly beneath the epithelia, are present.

The epithelium of the outer surfaces consists of cuboidal cells and is rich in unicellular glands. It does not seem to be ciliated, apart from dubious indications of scattered ciliated cells. The epithelium of the inner surfaces, on the other hand, is strongly ciliated, both on the ridges and the smooth areas, in connection with the functions of sorting and transport of food. The cilia are tall, much more so than those on the epithelia of the foot and mantle, and vary in height in different regions (Fig. 7). The tallest ones are on that area of the smooth portion approaching the mouth (Fig. 7,*B*).

The epithelium of the inner surfaces varies in height, being tallest on the smooth portions. In the grooves between the ridges the epithelium is lowest on the dorsal walls and contains numerous gland cells (type *PB*, Fig. 7,*C*). At the bottom of the groove there is an abrupt transition to a taller epithelium on the

opposite (ventral) wall. The cilia are well developed on the ventral wall of the groove, but are apparently absent from the dorsal wall.

There are three kinds of gland cells which secrete on to the inner surfaces of the palps. They are designated as types *PA*, *PB*, and *PC*, the letter *P* indicating that they belong to the palps.

Type *PA* (Fig. 7,*B*) is present in the epithelium of the part of the smooth portion approaching the mouth. The cell body containing the nucleus lies in a basal position in the epithelium, and from it a narrow duct passes upwards between the epithelial cells to open on the surface. The cytoplasm contains a few small vacuoles, and is strongly P.A.S.-positive. The nucleus is large, spherical, and vesicular, with a nucleolus.

TABLE 3

STAINING REACTIONS OF GLAND CELLS IN THE LABIAL PALPS*

Stain	Type *PA*	Type *PB*	Type *PC*
Iron haematoxylin and mucicarmine	—	Colourless or black	Pink
Periodic acid–Schiff	Deep magenta	Colourless	Faint pink
Gomori's aldehyde–fuchsin	Purple	Colourless	Purple
Iron haematoxylin and phloxine	—	Pink or black	Colourless
Ehrlich's haematoxylin and phloxine	Pink	Bright pink	Light mauve
Azan	Pale pink	Red	Pale blue

* See also Figure 7, p. 230.

Type *PB* is found in both the smooth and ridged portions, mostly in the latter (Fig. 7,*C*) The secretion is in the form of large spherical droplets which stain red with azan but do not give a P.A.S. reaction. The cell body is goblet-shaped and is connected with the basement membrane by a slender stalk, the top of which is expanded into continuity with the perinuclear cytoplasm. The apical portion of the cell, above the nucleus, is swollen by the accumulated secretion.

The type *PC* cells stain pink with mucicarmine, and have vacuolated foamy cytoplasm (Fig. 7,*A*). The nucleus is compact and darkly staining, contrasting with the large nucleus of the *PA* cells. The *PC* cells occur on the tops of the ridges, where they are entirely intra-epithelial, and also in that part of the smooth portion immediately ventral to the ridged area. In the smooth portion they are very numerous, some being intra-epithelial but the majority forming a distinct subepithelial layer (Fig. 7,*D*).

The staining reactions of the *PA*, *PB*, and *PC* gland cells are listed in Table 3.

(*e*) *The Ctenidia*

The ctenidia consist of many filaments united to one another only by ciliary junctions (Fig. 8). The junctions can easily be separated, so that rough handling

causes fraying of the ctenidia. Each ctenidium consists of two hemibranchs and is W-shaped in transverse section (Fig. 2,*D*,*E*). Each filament consists of a descending portion and an ascending portion. The free end of the ascending portion is recurved. The recurved ends of the filaments are in alignment, and so form a groove at the level of the base of the ctenidium. In this groove, the feeding grove (Fig. 1,*B*; Fig. 2,*D*), a forwardly directed ciliary current conveys food particles to the labial palps.

The ctenidial filaments are supported on a suspensory membrane consisting principally of gelatinous connective tissue. In the suspensory membrane, at the bases of the filaments, is a strip of well-developed longitudinal muscle. A large nerve from the visceral ganglion passes down into the free tip of the suspensory membrane. Impulses transmitted along this nerve cause contraction of the longitudinal muscle, thus causing a ventral flexion of the free tip. It is possible that the ventral bending of the tip takes place at intervals so that material can be transferred from the ctenidium to the rejection point on the mantle. A similar free tip to the suspensory membrane of the ctenidium is present in the related forms *Arca tetragona* and *Glycymeris glycymeris* (Atkins 1936).

The filaments contain blood vessels, through which the blood flows while it is being oxygenated from the respiratory water current passing through the gaps between the filaments. The filaments are flattened, thus forming a large total surface area for gaseous exchange.

The filaments bear several sets of cilia (Fig. 8). On one edge there is a narrow tract of longish cilia, flanked on either side by a wide tract of shorter cilia. On each side there is a group of lateral cilia, which set up the respiratory current. There are extensively ciliary junctions, where long cilia of one filament interdigitate with cilia of its neighbour, thus holding the filaments together.

A comparison with the description and drawings by Atkins (1936) of the filaments in two species of the Arcidae reveals a marked difference between her species and *A. trapezia*, a difference which is probably significant in determining the relative efficiency of the sorting of particulate matter on the ctenidia. In *Arca tetragona* and *Glycymeris glycymeris* the tract of long ("coarse frontal") cilia is flanked by narrow tracts of short ("fine frontal") cilia. The tracts of fine frontal cilia are not nearly as extensive in these two species as they are in *A. trapezia*. The possible significance of the difference in ciliation is dealt with in Section IV.

(f) Ciliary Currents in the Mantle Cavity

The ciliary mechanisms and currents in the lamellibranch mantle cavity have been the subject of intensive study by a number of workers including Kellogg (1915) and Atkins (1936).

As the main interest during the present study has been the micro-anatomy and histology of the animal, only the general pattern of the ciliary currents has been examined, and finer details have not been investigated. The principal currents in the mantle cavity and on the palps are shown in Figure 3.

The ciliary currents on the foot and the mantle are concerned with the

removal of sand from the mantle cavity, while those on the ctenidia and palps function in sorting food from other particles introduced in suspension by the inhalant water current. The general pattern of the currents is similar to that in the two species of Arcidiae studied by Atkins (1936).

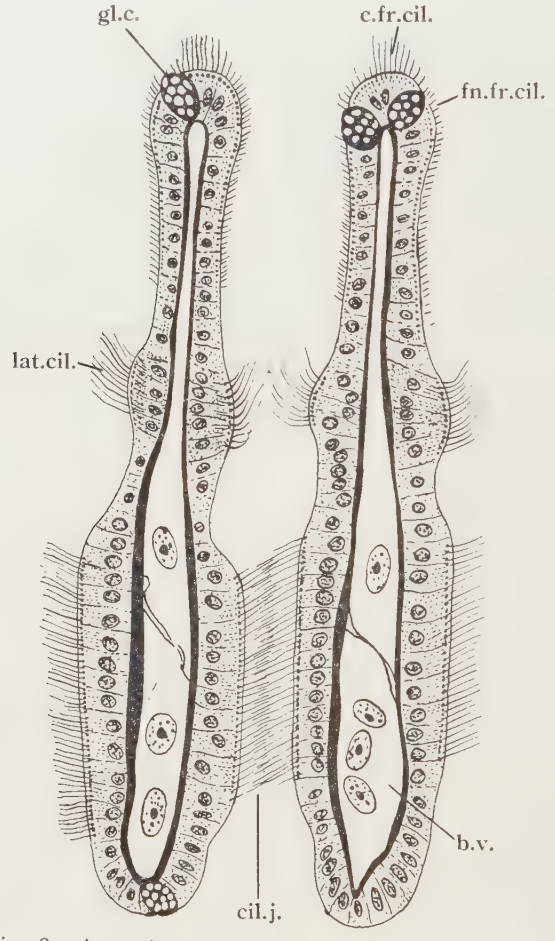

Fig. 8.—A section through two ctenidial filaments.

The ciliary currents on the ctenidia flow simultaneously in opposite directions, at least at times. When carmine particles were dropped on to the ctenidia, the large ones were carried ventralwards to the free edges (tailed arrows, Fig. 3,*A*), and the small ones travelled dorsalwards (small tailless arrows, Fig. 3,*A*). The large particles are moved by the action of the long frontal cilia, while the tracts of short cilia, beating in the opposite direction, send the small particles towards the feeding grooves at the tips of the filaments.

The current along the ventral edge of the ctenidium is a posteriorly directed rejection current. Atkins (1936) observed similarly directed currents in *Arca tetragona* and *Glycymeris glycymeris*. A current passing towards the posterior end,

along the ventral edge of the ctenidium, is found only in a small number of lamellibranchs. In the majority of species this current passes anteriorly towards the palps, and is therefore a feeding current.

On the foot and the mantle there are posteriorly directed currents which remove silt, thus keeping the mantle cavity clean (Fig. 3,*A*,*B*). On the mantle, at the level of the feeding groove of the ctenidium, there is a forwardly directed current; a posteriorly directed current at this level would work antagonistically to the feeding current. A similarly directed current is also present on the foot (Fig. 3,*C*). The principal rejection currents on the mantle converge posteriorly on a rejection point at the mantle edge. Particles carried along the ventral edge of the ctenidium are probably also cast off at this point, the free tip of the suspensory membrane being bent ventrally at intervals to touch the mantle at this point and transfer accumulated material to it.

On the labial palps, the ridged sorting areas are extensive (Fig. 3,*C*). The anteriorly directed current on the foot at the level of the feeding groove of the ctenidium would inevitably carry sand particles from time to time; this current does not pass onto the ridges, but is deflected onto the narrow flange formed by the posterior border of the inner palp. A ventrally directed current along this flange carries the particles to the rejection point.

On the ridged areas of the palps, food particles are sorted from unsuitable material. The food particles pass to the oral groove, along which they are carried towards the mouth.

(*g*) *The Musculature*

The musculature consists entirely of smooth fibres. There are two adductor muscles (Fig. 1). The posterior adductor is divided into a large anterior "fast" portion having a yellowish colour, and a smaller pearly white (nacreous) or "slow" portion of crescentic cross section (Fig. 1,*D*). The foot is provided with paired anterior and posterior pedal retractors, and has a complex intrinsic musculature. Occasional branching muscle fibres were observed in the foot.

The visceral mass has a muscular wall which is most complete laterally (Fig. 2,*C*); there is no clear line of demarcation between this and the muscles in the walls of the foot (Fig. 2,*D*). Dorsally, the muscular wall of the visceral mass is incomplete, being composed of scattered small muscles arising from the dorsal body surface in the area between the anterior adductor muscle and the pericardial cavity (Fig. 1,*C*).

In the mantle, as described above, the musculature is almost entirely confined to the border.

There is a well-developed longitudinal muscle in each ctenidial suspensory membrane. Immediately ventral to this muscle is a large blood vessel (Fig. 2,*E*) which carries blood from the ctenidial filaments to the heart.

Some muscle fibres are present in association with the stomach and other organs, but on the whole are not markedly organized into discrete muscles. Where

more definite muscles are formed by the aggregation of fibres, a connective tissue fibre investment of each muscle fibre (endomysium) can be distinguished.

Muscles which are attached to the shell, such as the adductors, the radial fibres of the mantle border, and the pedal retractors, are attached via a modified portion of the epithelium which is interposed between the shell and the body of the

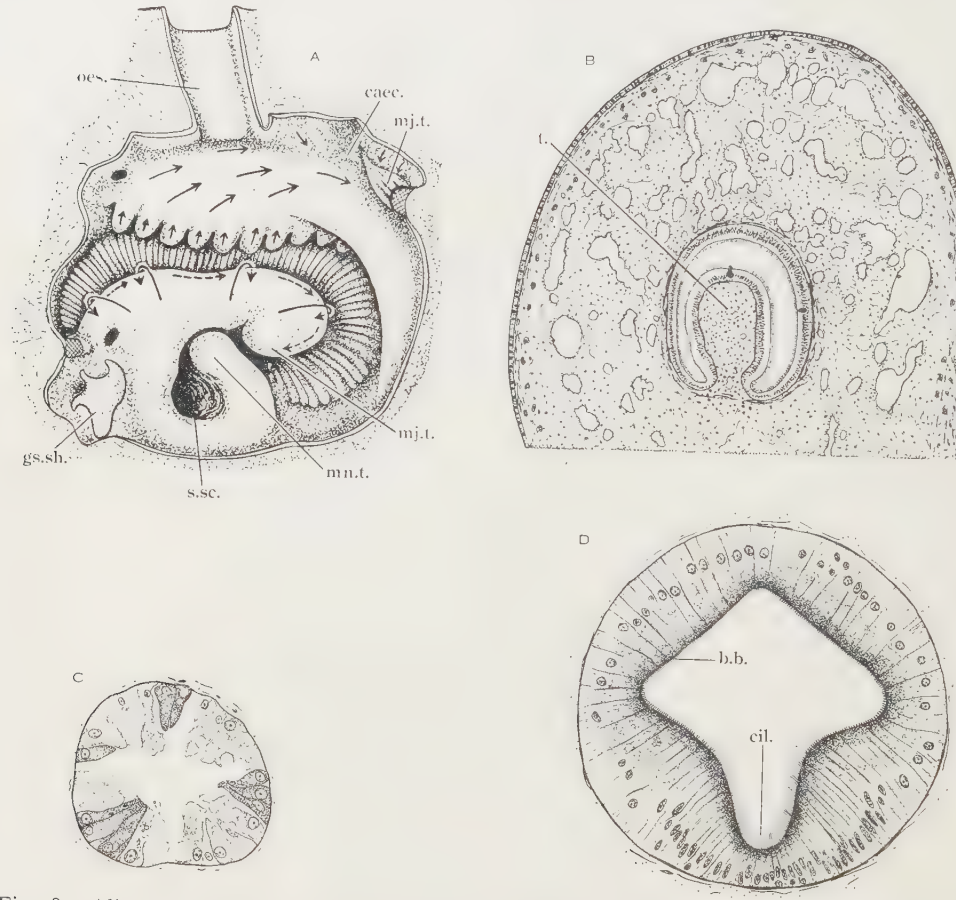

Fig. 9.—Alimentary system. *A*, dissection of stomach; *B*, low-power projection drawing through the rectum, showing typhlosole; *C*, camera lucida, oil-immersion drawing of a digestive tubule, showing vacuolated digestive cells and groups of darkly staining cells; *D*, camera lucida, oil-immersion drawing of a ciliated primary duct.

muscle. The epithelium rests on a distinct basement membrane which shows up well in sections treated by P.A.S. after pretreatment with saliva. The surface of the epithelium is covered by a pad of fibrous character which unites it to the shell.

The myofibrils appear to penetrate the epithelium to connect with the fibrous pad. According to Siebert (1913), in *Anodonta cellensis* the adductor muscle fibres pass through the epithelium to attach to the pad ("helle Schicht").

In sections of *A. trapezia* stained with iron haematoxylin, the muscle fibres were mostly coloured black, although some did not take up the stain. Under oil immersion, the fibres appeared to branch, the individual myofibrils penetrating the basement membrane and continuing across the epithelium to the fibrous pad; in a few places fine black fibres were seen crossing the epithelium and coming into continuity with the deeply stained muscle fibres. The basement membrane, although well developed, has an irregular and rather fuzzy outline, which would seem to be consistent with penetration by the myofibrils.

(*h*) *The Alimentary System*

The alimentary system consists of a short oesophagus, a stomach, with a caecum, style sac with crystalline style, intestine, and a mass of digestive tubules surrounding most of the stomach and connected with the latter by ducts. The oesophagus, the stomach (except that part bearing the gastric shield), and the intestine are lined by ciliated columnar epithelia rich in gland cells. Part of the roof (dorsal wall) of the stomach bears a firm gastric shield (Fig. 9,*A*). The caecum opens from the right anterior corner of the stomach. The apertures of the ducts to the digestive tubules lie mostly in a row passing diagonally across the stomach floor (ventral wall) from the left anterior corner to the right posterior. From its commencement in the caecum a prominent fold, the major typhlosole, passes across the stomach roof to the left side, turns downwards in the left wall, and continues back across the floor towards the right side as a prominent shelf overhanging the intestinal groove. It then curves posteriorly to approach the opening of the intestine. A large crystalline style projects into the lumen of the stomach from the style sac. Over the head of the style the epithelium of the stomach roof is covered by the gastric shield, a gelatinous cuticular structure which protects the underlying cells from abrasion by hard particles carried on the rotating style.

Between the intestinal groove (broken arrows, Fig. 9,*A*) and the row of openings to the digestive diverticula, the floor of the stomach is provided with many ridges; this is the sorting area of the stomach. The anterior portion of the stomach floor, immediately behind the opening of the oesophagus, is smooth.

The general pattern of ciliary currents in the stomach is shown in Figure 9,*A*. The current on the anterior portion of the floor is directed towards the caecum. Large particles dropped on the floor posterior to the sorting area are carried over the shelf formed by the major typhlosole and fall into the intestinal groove, to be carried to the intestine along the pathway indicated by the broken arrows.

In some sections the gastric shield shows horizontal stratification, indicating intermittent secretion by the epithelial cells. In P.A.S.-treated sections it colours pink, while in places below it there are groups of cells containing P.A.S.-positive granules. Figure 10,*A–F*, shows a number of camera lucida drawings indicating the distribution of the P.A.S.-positive material in the underlying epithelium, arranged as a series of secretion stages. All the drawings were made from sections of a single stomach. In *A* and *B*, clusters of granules are present at the

level of the nuclei, and a few small granules are scattered at the apical ends of the cells. Maximal secretion is evident in *B*. In *C*, the phase of synthesis appears to be ended, for the large granules are no longer evident and the pink material appears more diffuse. In *D* and *E* the secretion is migrating to the apical ends

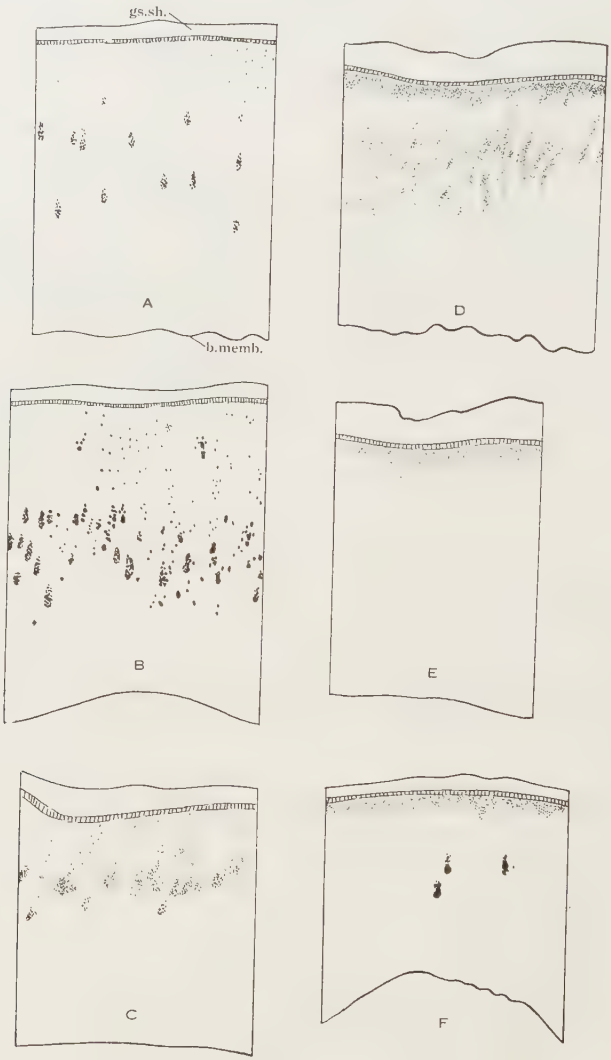

Fig. 10.—Camera lucida drawings of the distribution of P.A.S.-positive material in the epithelium under the gastric shield. Explanation in text.

of the cells. A comparison of the last three stages shows that the layer of accumulated material in the ends of the cells varies little in average thickness or density, indicating that it is being transferred to the shield simultaneously with the arrival in the layer of more secretion from below. In *F* a new cycle of

secretion is commencing, while there is yet some material from the preceding cycle present in the cells.

In other parts of the epithelium below the gastric shield, there was no indication of P.A.S.-positive material; the cells of these sites were not active in secretion at the time of fixation.

The lumen of the stomach is connected with the digestive tubules by means of a system of branching ducts, which may be distinguished as primary and secondary ducts, following the terminology of Owen (1955).

In the primary ducts there are cilia, which are confined to a groove (Fig. 9,*D*), the remainder of the cells which line the lumen being bounded by a brush border which gives a positive P.A.S. reaction. The nuclei of the brush border cells are spherical, those of the ciliated cells are elongated. The apical cytoplasm of both types of cell is rather more deeply staining than that of the remainder of the cell.

The ciliated primary ducts are connected with the digestive tubules by means of short non-ciliated secondary ducts.

The digestive tubules are blind sacs lined by vacuolated digestive cells among which are groups of somewhat smaller darkly staining cells. The nucleus in both types is spherical and vesicular, with a prominent nucleolus. The existence of two types of cells, one more deeply staining than the others, appears to be general in the lamellibranchs, for it has been observed in various species, including *Cardium edule* (Johnstone 1899, fig. 16), *Anodonta cellensis* (Gutheil 1912), *Ostrea edulis* (Yonge 1926), and others (Owen 1955).

In some preparations stained with iron haematoxylin, the free surfaces of some of the digestive cells show fine striations resembling a brush border. They are not present all the time, being absent from those cells from which excretory spheres are being constricted off. A similar striation was observed by Owen (1956) in the digestive tubules of Nuculidae.

Muscle fibres are present in the connective tissue around the ducts, but do not appear to be present around the digestive tubules.

The intestine and style sac open from the posterior part of the stomach floor, and their lumina are in communication via a slit bounded by the major and minor typhlosoles. The intestine descends into the foot, where it describes a double loop (Fig. 1,*D*) and then ascends parallel to and on the right of the descending portion. Passing to the right of the stomach, it then comes over into the mid-line. The rectum, which has a prominent ventral typhlosole (Fig. 9,*B*), traverses the ventricle of the heart and then passes dorsal to the posterior adductor muscle to terminate at the anus. The rectum is surrounded by a few circularly arranged muscle fibres. Near the anus, subepithelial mucous glands are present in the connective tissue surrounding the rectum. These glands discharge into the rectum, their secretion presumably serving to bind the faeces together into pellets before they are voided. The rectum is the only site in the entire alimentary tract where there are sub-epithelial glands secreting into the lumen; gland cells are abundant in all regions but except for those around the rectum they are entirely intra-epithelial.

(*i*) *The Vascular System*

The heart consists of a single median ventricle and two lateral auricles. A large anterior aorta arises from the ventricle in the mid-line and then diverges to the right (Fig. 1,*C*; Fig. 2,*D*). As there is no corresponding vessel on the left side, this part of the vascular system displays asymmetry.

The protrusible foot can be extended by blood flowing into it, presumably as a result of contraction of the muscles in the body walls of the visceral mass. The blood acts as a "haemoskeleton" filling the spaces in the foot. When the foot is fully extended, its surface is smooth as a result of fluid pressure within (Fig. 1,*A*). When it is retracted, its surface appears wrinkled (Fig. 1,*B*). The foot can be withdrawn quickly by contraction of its musculature. If a live animal is bisected by a median sagittal cut, the pedal ganglion is exposed. When the ganglion is touched with a needle, there is a violent contraction of much of its musculature. On contraction of the foot, the blood is squeezed out of the vascular spaces into the visceral mass, whose body wall muscles presumably relax simultaneously with the contraction of the foot muscles to allow the blood to flow into the visceral mass.

After oxygenation in the ctenidia, the blood passes to the heart and is distributed once again to the body.

(*j*) *The Reproductive System*

The sexes are separate. In the summer months preceding spawning, the female can be identified by the brilliant orange colour of the ovaries. If the male is opened and the body surface is cut or torn, the contents of the testes ooze out as a thick white fluid. The time of spawning is in the late summer.

The oviducts are lined by a strongly ciliated epithelium containing unicellular glands (Fig. 12,*B*). The histology of the oviduct resembles that of *Anodonta*, which was described by Weisensee (1916).

The oviduct and kidney open by a common pore situated on the tip of a small papilla on each side (Fig. 12,*A*).

(*k*) *The Kidneys*

The kidneys are situated posterior to the auricles of the heart (Fig. 1,*C*). They consist of branched tubules of ciliated cuboidal or low columnar epithelium whose nuclei are compact and darkly staining with haematoxylin. The nuclei are also P.A.S.-positive, a feature which is shared with the nuclei of the amoebocytes. The tubules are surrounded by loose connective tissue and blood spaces. Embedded in the connective tissue are numerous large cells packed with coarse brown granules (Fig. 12,*C*). These "granule cells" are found elsewhere in the body in comparatively small numbers, but are especially abundant in the neighbourhood of the kidney tubules. Similar cells have been observed in association with the kidney of the snail *Helix pomatia* (Freitag 1916) as well as in the general connective tissue of the same species (Kisker 1923).

The kidney tubules of each side are connected with the pericardial cavity by means of a renopericardial canal. The canal is lined by tall columnar cells with a dense investment of very long cilia (Fig. 12,*D*). The nuclei of the cells are large, spherical, and vesicular, and each has a prominent nucleolus. They are much larger than the nuclei of the cells lining the kidney tubules.

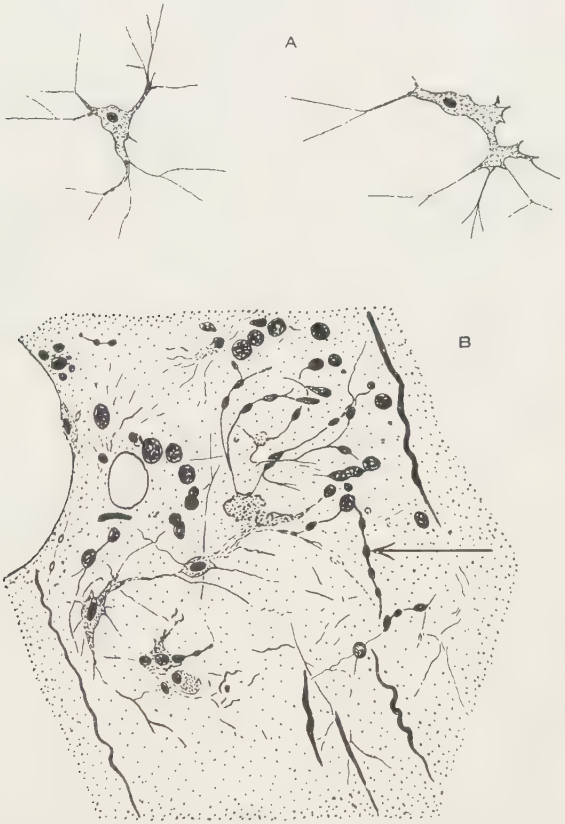

Fig. 11.—Cells of connective tissue. *A*, camera lucida drawings of two stellate cells; *B*, stellate cells and translucent granules. The granules are often in rows (arrow).

(*l*) *Connective Tissue and Blood Cells*

The connective tissue is composed of a gelatinous ground substance or matrix in which fibres, cells, and granules of various kinds are embedded. It forms a packing around the viscera and makes up the bulk of certain organs, such as the ctenidial suspensory membranes and the palps.

There is a well-developed fibrous component which, in suitably stained preparations, appears as a network of fibres of various thicknesses down to the limits of visibility. Between the muscle fibres it forms endomysium, and it is concentrated in the basement membranes of the epithelia. The basement membranes give a strong P.A.S. reaction. The fibrous component of the connective tissue,

including the basement membrane, stains blue with azan, indicating the presence of collagen.

Two kinds of connective tissue cells can be distinguished in *A. trapezia*. They are (1) stellate connective tissue cells, and (2) "granule" cells.

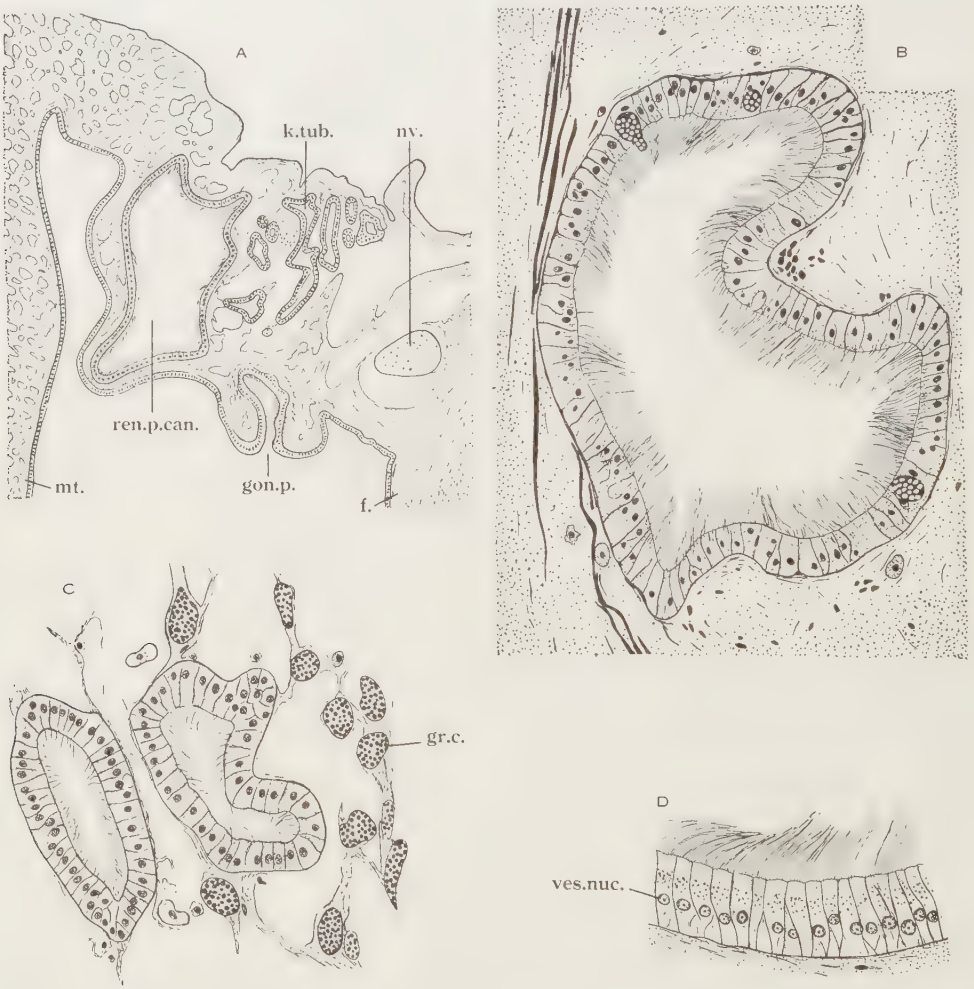

Fig. 12.—Histology of oviduct, kidney, and renopericardial canal. *A*, projection drawing of a section through the kidney region; *B*, oviduct; *C*, kidney tubules and granule cells; *D*, renopericardial canal epithelium. (*B*, *C*, and *D* all to same scale.)

In the connective tissues of molluscs, three principal varieties of cells have been described. They are the two kinds found in *A. trapezia*, as well as large vesicular cells with a glycogen-storing function, the Leydig's cells. The literature contains a variety of synonyms (see Section IV), and the relationships between the various connective tissue and blood cells are not well understood.

In *A. trapezia,* embedded in the ground substance are stellate cells (Fig. 11,*A*). The cell body, surrounding the compact nucleus, gives off a number of branching processes which extend for considerable distances as attenuated threads. The cytoplasm may be quite granular or relatively free of granules; there is considerable individual variation in this respect.

Stellate cells have been observed in a number of species of molluscs by several different workers. They have been thoroughly described in *Helix pomatia* by Kisker (1923). It is probable that they are universal throughout the phylum.

The other type of cell found in *A. trapezia* is larger than the body of the stellate cell. It is usually of spherical or ovoid form, and is laden with large brownish spherical granules. It occurs in large numbers in the connective tissue around the kidney tubules (Fig. 12,*C*). Similar cells have been described in other molluscs under a variety of names, and agreement about their functions is lacking (see Section IV). In this paper, the term "granule cell" is used in referring to them.

The large vesicular Leydig's cells which have been studied in other molluscs such as the snail and the oyster, and which in these forms store glycogen, do not appear to be present in *A. trapezia.*

In *A. trapezia,* glycogen is present as granules of varying sizes scattered throughout the gelatinous connective tissue matrix. No obvious relation to cells can be demonstrated. There are in some places slight suggestions that some of the granules may be arranged in sequence like beads on a string, as if they have been deposited in the fine processes of stellate cells.

Peculiar translucent granules of varying shape and size are found in considerable numbers in the connective tissue of the mantle border, the free tips of the ctenidial suspensory membranes, etc. They are restricted to the posterior end of the animal. Often they are in rows, like a string of beads (Fig. 11,*B*, arrow), and appear to be formed in the processes of stellate cells. Their composition is not known; tests with the P.A.S. reaction show that they are not glycogen. With Ehrlich's haematoxylin and phloxine they remain colourless. They stain red with azan and purple with Gomori's aldehyde–fuchsin. They are mostly confined to the connective tissue, but some are present in the epithelium of the abdominal sense organ, suggesting that processes of the stellate cells penetrate into the epithelium.

Examination of fresh specimens reveals a whitish mottling of the mantle border and of free tips of the suspensory membranes of the ctenidia and neighbouring tissues. The distribution of the whitish patches corresponds with that of the translucent granules as seen in sections. The granules are present in those tissues which would be likely to have light falling on them from time to time, suggesting that they are formed in response to illumination. Atkins (1936) observed whitish patches in *Glycymeris glycymeris,* in regions which she considered likely to be reached by light.

In the circulating blood there are two kinds of cells, the leucocytes (amoebocytes) and the erythrocytes.

The erythrocytes are circular, apparently biconcave, disks. Their form was first observed by Tenison-Woods (1888). Each has a nucleus, and the cytoplasm

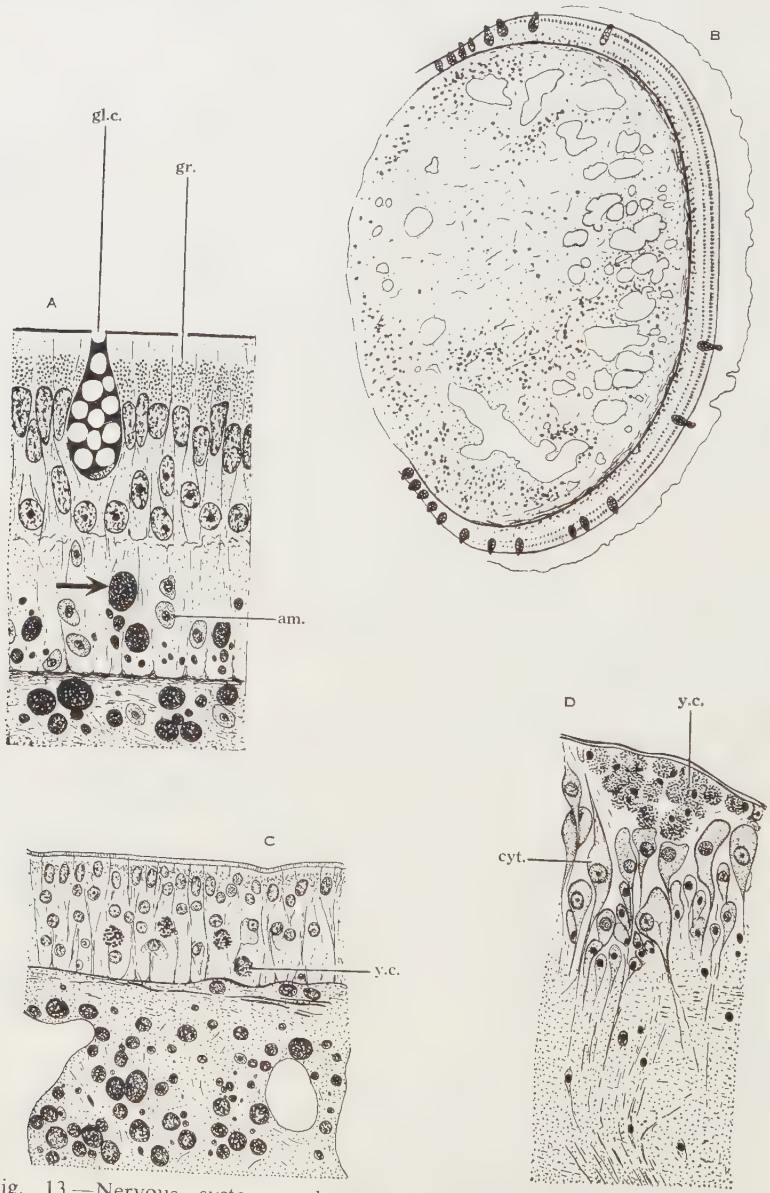

Fig. 13.—Nervous system and sense organs. *A*, epithelium of the abdominal sense organ. The arrow indicates a translucent granule; *B*, low-power projection drawing of the abdominal sense organ; *C*, portion of the osphradium; *D*, nerve cell cytons and yellow cells in a ganglion.

contains a variable number of coarse dark granules. When the blood is drawn and placed on a slide and examined under the microscope immediately, the discoidal

shape of the erythrocytes is recognizable. However, within a very short time (1–2 min), the cells have taken on a crenated spherical form. There is no tendency to form rouleaux after the manner of mammalian erythrocytes. The red pigment is haemoglobin (Cleland, personal communication).

The erythrocytes are in all respects similar to those of *Arca inflata*, which were described by Sato (1931).

Immediately the blood is extracted, the amoebocytes clump together. This behaviour is a regular occurrence with molluscan leucocytes, having been observed in a number of species, including *Ostrea edulis* (Takatsuki 1934), *Pecten* (Dakin 1909), and *Okadaia elegans* (Baba 1937).

Amoebocytes laden with brown granules are present in large numbers around the alimentary tract. Elsewhere, amoebocytes are found migrating between epithelial cells of various organs, such as the palp, etc. (Fig. 7,*A*,*B*; Fig. 13,*A*).

(*m*) *Nervous System and Sense Organs*

There are three pairs of ganglia: cerebropleural, pedal, and visceral. The palps and the anterior portion of the mantle are innervated by the cerebropleural ganglia which are situated ventrolateral to the oesophagus. The pedal ganglia are fused in the mid-line and lie ventral to the stomach. A nerve trunk connects each pedal ganglion with the cerebropleural ganglion of the same side. From each pedal ganglion a large nerve trunk passes downwards into the foot, and several smaller trunks pass to the intestinal region. A longitudinal trunk connects each cerebropleural ganglion to the visceral ganglion, which lies immediately beneath the epithelium of the ventral body surface posterior to the foot. From each visceral ganglion, nerves pass to the mantle, the free tips of the ctenidial suspensory membranes, etc.

Within the ganglia, the cytons are peripheral and the interior is occupied by nerve fibres (Fig. 13,*D*). The cytons vary in size; in the larger ones the nuclei are large, spherical, and vesicular, usually with a distinct nucleolus, while in the smaller cytons the nuclei are small, compact, and darkly staining.

In all the ganglia there are clusters of yellow cells with coarsely granular cytoplasm and compact, darkly staining nuclei (Fig. 13,*D*). The yellow cells lie immediately inside the connective tissue capsule of the ganglion, never deep in the interior. Their size is comparable with that of amoebocytes. Their function is not known, but it is possible that they are amoebocytes in which metabolic wastes from the neurones have accumulated, or they may be endocrine cells.

The osphradium (Fig. 13,*C*) is a thickening of the epithelium in the vicinity of the visceral ganglia and the bases of the nerves to the ctenidial suspensory membranes. In places, nerve fibres can be seen entering it. There are two kinds of cells in it: (1) the columnar epithelial cells of the surface layer; (2) underlying nervous elements or ganglion cells. Scattered yellow cells of the kind described above for the ganglia are also present. The cytoplasm of the epithelial cells contains yellowish pigment granules above the ovoid nuclei. Below the nucleus, each epithelial cell narrows down to an elongated thread which passes down

through the ganglion cell layer to meet the basement membrane. The ganglion cell nuclei are spherical and vesicular, each having a distinct nucleolus. It was possible to find an occasional multipolar ganglion cell, but it was not determined whether such cells are very numerous. Processes of the ganglion cells pass between the columnar epithelial cells and approach the surface. This last finding is in agreement with those of Pelseneer (1891), who described the histology of the lamellibranch osphradium in the following words:

> "Un revêtement ganglionnaire au-dessus duquel l'epithélium de la cavité palléale est modifiée en cellules élevées et ciliées; entre celles-ci se trouvent des terminaisons nerveuses continues avec les prolongements des cellules ganglionnaires."

In sections, the osphradium of *A. trapezia* is covered by a layer with the appearance of a brush order, and it was not certain, apart from scattered dubious suggestions, that cilia were present, as claimed by Pelseneer for his material. There may be differences between species in this regard, for Dakin (1909) stated that the osphradium of *Pecten* bore a prominent cuticle and that there were no cilia on its cells even though they were present on the adjacent ordinary epithelium.

Near the anus there are two small swellings. Similar structures are present in other lamellibranchs, including *Arca noae*, in which they are innervated by branches of the posterior mantle nerves (Thiele 1889). Thiele named these structures "abdominal sense organs". Each abdominal sense organ in *A. trapezia* is a rounded swelling covered by a thickened epithelium with the nuclei in two layers (Fig. 13,*A*,*B*). The epithelium bears an investment of long flagella, which in the living organ examined under the microscope can be seen in constant motion. They are very delicate and disintegrate on fixation to give an appearance suggestive of a secreted layer consisting of fine anastomosing threads. The impression was heightened in a section which had been stained with Gomori's aldehyde–fuchsin, for the "threads" were stained purple, as also were the coarse granules in the cytoplasm of the epithelial cells, a circumstance which seemed to suggest that the granules represented secretion still to be extruded. Examination of the live organ revealed that the appearance of the threads was an artefact. Dakin (1909) examined the abdominal sense organ in *Pecten* and observed the long flagella ("cilia") which he regarded as the terminations of primitive neurofibrillae, for he found them to be continuations of fine nerve fibrils. The precise function of the abdominal sense organ is uncertain. Thiele (1889) suggested that it perceived vibrations in the water.

There are scattered gland cells in the abdominal sense organ of *A. trapezia* (Fig. 13,*A*,*B*). The secretion stains red with azan. The glands are sparse over most of the organ, but are more abundant at the periphery and in the adjacent epithelia. Thiele and Dakin do not say whether gland cells are present in any of their examples.

In some species of *Arcidae*, small hemispherical compound eyes are present in the mantle border; those of *Arca noae* were described by Hesse (1900). Such eyes do not appear to be present in *A. trapezia*.

IV. Discussion

(*a*) *Alimentary System*

The anatomy of the stomach is closely similar to that of the related genus *Glycymeris*, which was described by Graham (1949).

The digestive diverticula consist of ciliated primary and non-ciliated secondary ducts, plus blind digestive tubules. The appearance of a primary duct in cross section (Fig. 9,*D*) appears identical with that illustrated by Owen (1955) for *Mytilus edulis*. Owen found that the cilia of the primary duct were also confined to a groove in *Zirphaea crispata* and *Ostrea edulis*, and suggested that this feature was probably universal in the Anisomyaria and Eulamellibranchia. In the three species examined he found that the cilia beat in the direction of the stomach, setting up an exhalant current. Since the ducts and tubules form a closed fluid system, he concluded that there was an inhalant counter-current in the non-ciliated portion of the primary duct. Small particles of food would be carried towards the tubules in this current, while excretory material would be transported from the tubules to the stomach in the exhalant current.

Among the digestive cells in the tubules there are groups of smaller darkly staining cells (Fig. 9,*C*). Flagella are borne by the darkly staining cells in many species of lamellibranchs, if not in all (Owen 1955). In the literature they have been noted by several workers, and are usually called cilia, but Owen presents reasons for calling them flagella (Owen 1956). They could not be identified with certainty in my sections of *A. trapezia*. They appear to be sensitive to the action of fixatives, for similar difficulty in finding them in fixed and sectioned material was experienced by several workers, including Yonge (1926) who stated that they were not present in sections of *Ostrea edulis* although they could be seen beating in tubules from fresh material. Yonge concluded that "there is strong presumptive evidence that cilia are present in the tubules of all lamellibranchs". They are probably present in the tubules of *A. trapezia*.

In a number of species, there are muscle fibres around the digestive tubules (Owen 1955). They appear to be entirely absent from this situation in *A. trapezia*; they are, however, present around the ducts to the tubules. Yonge (1926) stated that in *Ostrea edulis*, the tubules were surrounded by connective tissue strands but muscle was not present. In this respect, *A. trapezia* appears to resemble the adult oyster. Quite recently Millar (1955) has shown that each digestive diverticulum of the larval oyster has a slender muscle passing round it, and that particles are drawn into the diverticula and returned to the stomach by rhythmical expansion and contraction of the diverticula. It would appear that the development of muscle fibres in relation to the digestive tubules of lamellibranch varies according to the species, no muscle being present around the tubules in *A. trapezia* and in the adult oyster.

The gastric shield is a cuticular secretion of the underlying epithelial cells (Fig. 10), the positive P.A.S. reaction of the secretion indicating a carbohydrate component. There have been several views expressed in the literature concerning its formation. Pelseneer (1891) mentions it as "un revêtement cuticulaire . . .

protégeant l'epithélium sécréteur qui l'a produit". Johnstone (1899) observed that it was stratified in *Cardium*, and regarded it as a secretion in which the cilia were embedded. Gutheil (1912) described the gastric shield of *Anodonta* as having a layered structure, and also considered it to be a secreted structure ("Secretbelag"). Yonge (1926) believed that it was not secreted but formed by the fusion of cilia, for he did not find any evidence of secretion in his sections of *Ostrea*. Pilgrim (1947) referred to the suggestion of Berkeley (1935) that the crystalline style lost its glucuronic and sulphuric acids, and that the remaining acetylglucosamine polymerized to form chitin. Pilgrim confirmed the van Wisselingh test for the gastric shield of *Diplodon*, but found that in the initial boiling with KOH "the size of the shield was considerably reduced, indicating some other substance beyond chitin" and suggested that the shield may consist of chitin and a protein, for Millon's reaction gave a brick red colour. It is evident from the sections of *Anadara* gastric shield and underlying epithelium that the shield is in fact secreted by the epithelial cells. The stratification is an indication of intermittent secretion. In its thicker parts the height of the shield is considerably greater than that of any of the cilia in the stomach, a feature which is not in accordance with Yonge's view that the shield is formed of fused cilia.

(*b*) *Ciliary Currents on the Ctenidia and Labial Palps*

The pattern of ciliary currents resembles that of *Glycymeris glycymeris* and *Arca tetragona* (Atkins 1936). In particular, there is a backwardly directed current along the ventral edge of each ctenidium, a condition not found in the majority of lamellibranchs but existing in many, if not all, Arcidae. The mechanism of sorting on the ctenidia was discussed by Atkins, who drew attention to the presence of two kinds of frontal cilia on the edges of the filaments, namely longer "coarse" and shorter "fine" frontal cilia. The coarse frontal cilia beat ventralwards and the fine frontal cilia beat dorsalwards, and, according to Atkins, the former are fully active only when stimulated by large particles falling on the filaments. When moderate amounts of suspended matter, consisting of food and silt particles mixed indiscriminately, are present the coarse and fine tracts beat in opposite directions simultaneously, presumably without interfering unduly with each other's water currents. This appears to be a very efficient sorting mechanism, which prevents most of the unsuitable material from reaching the feeding currents at the bases of the ctenidia.

Atkins remarked on the small number of palp ridges in the two species she examined. In *Arca tetragona* there are about 12 ridges on each palp, while *Glycymeris glycymeris* has only 1–3. This reduction of the sorting area on the palps was suggested as being due to the presence of a very efficient ctenidial sorting mechanism, which rendered an extensive palp sorting area unnecessary.

In *A. trapezia* there are about 36 ridges on each palp so that the sorting area is well developed. In all other respects the structure of the palps resembles that of Atkins' species.

On preliminary examination the sorting mechanism on the ctenidia appears to be very efficient in *A. trapezia*, as indicated by the movements of carmine

particles of various sizes. The presence of numerous ridges on the palps would at first sight appear to be inconsistent with Atkins' view. However, the structure of the ctenidial filaments differs significantly from that of her examples. As her figure 14 indicates, the tracts of fine frontal cilia are quite narrow. In *A. trapezia* the corresponding tracts are much wider, and the portion of the filament between the lateral cilia and the edge bearing the coarse frontal cilia is enlarged to accommodate them.

This difference in the width of the tracts of fine cilia could possibly explain the need for a larger number of palp ridges in *A. trapezia*. In Atkins' species, at times when the water entering the mantle cavity is heavily laden with sediment, the coarse frontal cilia would be stimulated to intense activity. Hydrodynamic competition would suppress the water currents set up by the fine frontal cilia. When the amount of coarse material falling on the filaments is less, the current set up by the coarse frontal cilia would be more gentle, so that the dorsally directed currents set up by the fine frontal cilia would not be inhibited. Under conditions where moderate amounts of coarse matter enter the mantle cavity, both dorsal and ventral currents would be flowing, and efficient sorting would proceed. Only a small sorting area would be needed on the palps to deal with the few unsuitable particles which escape sorting on the ctenidia.

In *A. trapezia*, when the water contains a lot of sediment, the coarse frontal cilia would be fully active. In this species, since the tracts of fine cilia are much wider, the suppressing effect of hydrodynamic competition would be limited to the zones immediately adjacent to the coarse frontal cilia; the currents set up by the fine cilia beyond these zones would continue to flow. Some coarse particles which failed to be removed by the coarse cilia would fall into the dorsally directed water currents and so pass to the feeding grooves and thence to the palps. A larger sorting area would therefore be required on the palps. The presence of *c.* 36 ridges appears to be associated with a ctenidial sorting mechanism which is less efficient than in Atkins' species. Atkins' view that the reduction in size of the sorting area on the palps of her examples is correlated with the efficiency of sorting on the ctenidia is supported by the present findings in *A. trapezia*.

An inspection of Atkins' text-figures 11 and 12 suggests that the relative area of the ctenidia is somewhat greater in the more elongated *Arca tetragona* than in the other species. It may be that in the former a greater amount of unsuitable material would reach the palps; hence the presence of *c.* 12 ridges as compared with at most three in *Glycymeris glycymeris*. This circumstance, although not commented on by Atkins, would appear to give further support to her suggestion.

Her comment that shell gravel is the normal habit of *Glycymeris glycymeris* also appears relevant. Such a habitat would presumably be less muddy than the situation where *A. trapezia* lives. Consequently there would be less likelihood of silt in large quantities entering the mantle cavity of the former. Of the three species at present under consideration *Glycymeris glycymeris* would appear to be the one least in need of a large number of palp ridges, partly on account of its habitat

and partly as a result of the relatively smaller area of ctenidium on which particles may fall.

(c) *Gland Cells*

The *MA* and *MB* gland cells of the mantle border both stain pink with mucicarmine and metachromatically with thionin, indicating acid mucopolysaccharides. The cytoplasm of the *MA* cells appears vacuolated and foamy, while that of the *MB* cells is non-vacuolated, coarsely granular, and strongly P.A.S.-positive. The *MA* cells are especially abundant close to the edge. They supply mucus which traps sand particles. The strong ciliary current parallel to the edge carries the mucus-entrapped particles to the mantle rejection point. The mucus must be tacky so that the particles may be held by it.

The *MB* glands secrete on to the outer surface of the mantle border, into the space between the epithelium and the shell. The periostracum acts as a barrier to the entry of sand grains, hence cilia are not present on the outer epithelium as there is no need of a mechanism for removing particles. The *MB* cells are therefore on functional grounds unlikely to be concerned with the production of tacky mucus of the type suitable for capturing particulate matter. The different appearance of their cytoplasm from that of the *MA* glands also suggests a difference in the nature of the secretion.

It appears likely that the *MB* cells secrete a lubricant, their mucous secretion being smooth and slippery rather than tacky. The mantle border can be retracted by the contraction of its radial muscle fibres. The *MB* cells probably form a lubricating mucus which facilitates smooth movement of the mantle border against the shell. As shown in Figure 4,*B*, the *MB* cells are present in the whole extent of the border, from the pallial attachment to the edge. Towards the edge they are more numerous, presumably an adaptation to supply greater quantities of mucus for lubricating that part of the mantle border which moves over the greatest distance during retraction.

A small number of *MC* cells is present in the mantle border, and large numbers of similar, if not identical, cells are present in the outer epithelium of the central portion (Fig. 5,*B*). It is probable that they are concerned in secretion of the shell. In *Ostrea edulis*, according to Korringa (1952), the epithelial cells deposit conchiolin, and "calcium is secreted by the 'mucus' glands which occur in great numbers between the epithelial cells".

In the foot, the *FA* cells, opening into the deeper portion of the groove, do not stain pink with mucicarmine, nor do they display metachromasia with thionin. They may be byssus glands; however, the author has not observed a byssus in any of his specimens. According to Atkins (1936) a byssus is present in *Arca* but not in *Glycymeris*.

The *FB* and *FC* cells stain with mucicarmine and show metachromasia with thionin. The *FC* cells, which, together with FB_2 cells, discharge on to the lateral surfaces of the foot, are strongly P.A.S.-positive and appear less vacuolated than the *FB* glands. The FB_1 cells are very abundant, and their secretion is undoubtedly an aid to burrowing. According to Atkins (1936), a creeping *Arca*

tetragona leaves a thick trail of mucus, and a *Glycymeris*, when beginning to burrow, was observed to produce much mucus which cemented the sand grains together. Like the *MA* cells of the mantle, the *FB* cells have vacuolated cytoplasm. Both types possibly form a tacky mucus in which sand particles may be firmly held.

The FB_2 cells are similar to the FB_1 cells except for their smaller size. They are intermingled with the *FC* cells (Fig. 6,*A*). It is not known whether the FB_2 and *FC* cells are two separate kinds differing in the composition or viscosity of their secretion or whether they represent different states of a single type. It seems probable that the former alternative is the true one; that the FB_2 cells secrete a tacky mucus for capturing particles which can then be removed by ciliary currents, while the *FC* cells, which resemble the *MB* cells in their strong P.A.S. reaction may, like the *MB* cells, be regarded as lubricating glands. The foot can be protruded beyond the edge of the shell. The friction of the surface of the organ against the shell would be minimized by a lubricating mucus.

Of the three types of gland cells which secrete on to the inner surfaces of the palps, type *PC* (Fig. 7,*A*,*D*) most resembles the *MA* and *FB* cells, and like them may be assumed to secrete a tacky mucus. The *PB* glands (Fig. 7,*C*), which are concentrated in the grooves of the ridged portion, are found scattered elsewhere in small numbers (Fig. 7, *A*,*B*). The most striking feature of the *PC* cells is their concentration in an extensive subepithelial layer in that part of the smooth portion immediately adjacent to the ridged area. In the part of the smooth portion approaching the mouth this subepithelial layer is absent. A possible explanation of this feature is afforded by a consideration of the functioning of the palps. Sorting takes place on the ridges. Food particles are caught up in mucus from the *PC* cells on the tops of the ridges, while many of the unsuitable particles fall into the grooves. Ciliary currents convey the food-laden mucus to the oral groove. Too many *PC* cells on the ridges would result in the excessive quantity of mucus trapping large numbers of unsuitable particles, hence their number is limited in this region. Owing to the limited amount of mucus, the food particles would be loosely held, and there would be a risk of many of them being lost. A source of additional mucus is provided by the development of large numbers of *PC* gland cells in the smooth portion, so that the food particles can be quickly bound together as soon as they leave the sorting area. If these glands were solely intra-epithelial, they might be unable to meet the demands when large amounts are required, hence they have become more numerous and encroached on the subepithelial tissues.

The food-laden mucus is carried over that part of the smooth portion containing the P.A.S.-positive *PA* cells. In the case of the P.A.S.-positive *MB* and *FC* glands, we can assume on functional grounds that a lubricant type of mucus is produced. The same assumption can be made for the *PA* cells. A lubricating secretion might facilitate rapid transport of the food over the remaining distance to the mouth. In all three organs, foot, mantle, and palps, there are gland cells with non-vacuolated or only slightly vacuolated cytoplasm and a very marked P.A.S. reaction in situations where a lubricant might be expected. Where a tacky

mucus is required, the cytoplasm appears vacuolated and only a weak P.A.S. reaction is given.

A. trapezia differs from some other lamellibranchs which have been described, so far as the glandular cells in the palps are concerned. In *Ostrea edulis,* Yonge (1926) observed mucous glands of the goblet type, which were located "almost exclusively near the summits of the folds". Siebert (1913) did not show any gland cells in his illustration of a section through a palp ridge of *Anodonta cellensis,* and remarked that mucous glands were present in the ridged portion only in very small numbers.

Concerning the layer of subepithelial gland cells in the smooth portion of the palps, Siebert refers to the earlier observations of List on *Mytilus galloprovincialis* and *Lithophagus lithophagus,* where such a layer was reported. He remarked on a similar appearance in *Anodonta cellensis,* which he illustrated in his figure 29. However, he stated that this alleged glandular layer consisted of wandering cells and calcium deposits, and denied the presence of subepithelial gland cells in the palps of *Anodonta cellensis.* He apparently overlooked the ducts and was thus led to this conclusion. Certainly, the ducts do not show well with the usual stains such as Ehrlich's haematoxylin and phloxine. With Gomori's aldehyde fuchsin they show up very clearly in *A. trapezia.* The present author's observations agree with those of List and not with those of Siebert.

If, as Siebert claims for his material, there is an aggregation of wandering cells and calcium deposits in this part of the palps, it must have some functional significance. The present author saw no such indication in his material. It seems likely that the explanation of Siebert's observation lies in three circumstances: (1) the role of calcium as a component of mucus; (2) the fact that *Anodonta cellensis* is a freshwater form while List's examples and *A. trapezia* are marine; (3) the function of "wandering cells" (amoebocytes) in the transport of calcium. Fretter (1952) suggested that calcium is an important component of mucus, for she says

> "the mucus of a snail (Prenant 1924) and of a slug contains calcium which is said to be present as the carbonate . . . Robertson (1914) regards the calcium present in mucus as an excretion of excess calcium absorbed with the food. It is perhaps better to think of it as an essential part of the secretion. Divalent ions such as calcium and magnesium stabilize intercellular matrices and the surfaces and mucous coverings of cells and organisms. So the calcium in the mucus of the pedal gland would prevent the immediate dispersion of this secretion, which is poured out to make a pathway for the animal, and must remain tacky for a while to secure it a foothold. In *Procerodes* calcium for this purpose is provided by the seawater (Weil and Pantin 1913) and without it the mucus, as an aid to locomotion, is ineffective. The land pulmonate must provide its own calcium, and this may be stored as carbonate or phosphate".

In the snail, calcium taken in with the food accumulates in the lime cells of the digestive gland, whence it is transported to other parts of the body by amoebocytes (Wagge 1951).

If the mucus formed by the *PC* cells in *A. trapezia* is to remain tacky, the necessary calcium ions will be present in the ambient sea-water. In the freshwater

form *Anodonta cellensis* the calcium would need to be taken in with the food, since it would not be present in sufficient amount in the water. The amoebocytes would transport it to the region of the gland cells in the palps, where it would be stored to be available as required. Probably it would be re-absorbed from the mucus after ingestion, and so conserved. In view of these considerations, Siebert's observations may perhaps be explained. It appears that his observation of calcium deposits and wandering cells is true, but he may have been mistaken in his belief that subepithelial glands were not present.

The viscosity of mucus probably depends on the function to be carried out, so that very tacky mucus is to be expected in some places and a more slippery secretion in other sites with different functional requirements. Such a difference was observed in *Haliotis* by Crofts (1929), who stated of the secretion of the pedal muclous glands,

> "It is much more viscid than the discharge from the hypobranchial glands and, unlike that, it forms a stiff stringy jelly after exposure to sea water. This helps in the early stages of adhesion . . . There is probably a difference between ordinary mucous and viscous secretion, as Thiele first suggested".

If the calcium in the mucus of the snail and slug is present as the carbonate, as has been suggested, it is difficult to understand how it would be ionized and so rendered effective in stabilizing the mucus. However, if Fretter's suggestion is correct, it would enable us to explain Siebert's discovery of calcium deposits around the mucous glands of the palps of *Anodonta*. It is difficult to see any other functional significance in the presence of calcium stores in this location.

(*d*) *Muscle Attachments*

At places such as the attachments of the adductor muscles to the shell, the epithelium is specially modified. So far as could be ascertained, the muscle fibre breaks up into its constituent myofibrils just below the basement membrane, and the myofibrils appear to penetrate the epithelium. A similar appearance was described by Siebert (1913) in *Anodonta cellensis*, but according to his description the muscle fibres penetrate *into* the epithelial cells ("Gute Schnitte lassen aber erkennen, dass die Muskelfasern nicht zwischen den Zellen des Epithels hindurchgehen und so an der Schale inserieren, sondern dass die Muskelbündel in die Zellen eindringen").

Whether the myofibrils actually penetrate into the epithelial cells or pass between them could not be determined in the sections of *A. trapezia*; indeed it was difficult to be certain that the myofibrils do actually penetrate the epithelium although the general appearance suggests that they do. Siebert's claim that the muscle fibres penetrate into the epithelial cells does not seem to be convincing, for it would seem more likely that they or the myofibrils would pass between the cells. It is possible that the myofibrils end at about the level of the basement membrane and attach to rod-like desmosomes which lie in the cell membranes. The question must remain open until it is settled by electron-microscopy.

(*e*) *Connective Tissue and Blood Cells*

The most striking features of the connective tissue of *A. trapezia* are (1) the apparent absence of Leydig's cells; (2) the storage of glycogen as granules scattered throughout the ground substance.

There is an extensive literature on the connective tissue cells of molluscs, but complete agreement about the relations, origin, and function of the cell types is lacking. Three principal types of cells are characteristic of molluscan connective tissues, and have been described under a variety of names. The three kinds are (1) Leydig's cells (Blasenzellen, Bindesubstanzzellen, Plasmazellen, Langersche Blasen or vésicules de Langer, Schleimzellen); (2) stellate cells (sternförmige Bindesubstanzzellen); (3) granule cells (Körnchenzellen, cellules mucoides, Kugelzellen, Mastzellen, Fettzellen, cellules sphéruleuses). The Leydig's cells have long been known to store glycogen, and their functions have been studied by numerous authors. There is rather less agreement about the granule cells, some authors regarding them as storage rather than excretory cells. Freitag (1916) and Kisker (1923) consider them to be storage cells. They are absent from a snail which has just been awakened from hibernation, but appear shortly after the animal is fed, perhaps arising from amoebocytes (Kisker 1923). In the oyster, there are "brownish granular cells" of phagocytic character in the pericardial epithelium and heart; these cells take up carmine particles and appear to play a part in excretion (Takatsuki 1934). From Takatsuki's description and his figure 12,*B* they would appear to be the same kind of cell as the granule cells which are so abundant around the kidney of *A. trapezia*. Takatsuki suggested that they sometimes received the particles from the amoebocytes.

The presence of large numbers of granule cells in the vicinity of the kidney, laden with large brownish granules, suggests that they have some functional relationship to excretion. If they are solely storage cells, one would expect them to be more evenly distributed throughout the body. It is, of course, quite possible that they are concerned with both functions, storage and excretion.

Cuénot (1892) stated that in aquatic pulmonates, the Leydig's cells are specialized into two kinds, one concerned with glycogen storage while the other type has phagocytic and excretory functions. In terrestrial pulmonates, he found only one kind of Leydig's cell, which was concerned with phagocytosis and excretion ("rein d'accumulation") in addition to storing glycogen. It is possible that a similar situation exists with regard to the granule cells; they may have an excretory function in some species and be storage cells in others, or might combine both activities.

In the absence (or rare occurrence?) of Leydig's cells in *A. trapezia*, the glycogen is scattered through the ground substance. It is possible that the stellate connective tissue cells carry out glycogen storage, the glycogen being deposited in the fine cytoplasmic extensions of the cells. In the majority of molluscs, it appears that specialized Leydig's cells have evolved, perhaps from modified stellate cells, and the stellate cells in these forms have probably themselves specialized in other directions and lost the function of storing glycogen. A comparative study

of the connective tissues of molluscs with a view to elucidating the specializations of the cell types in phylogeny, should prove of value.

There does not appear to be any specialized haemopoietic organ in *A. trapezia*. It is probable that the blood cells are formed in the general connective tissue. The amoebocytes resemble the stellate connective tissue cells in the variation in the quantity of granules contained in the cytoplasm. In *Helix aspersa*, Gatenby and Hill (1934) concluded that the cells in the connective tissue could be identified with the amoebocytes, and said "We do not at present believe that there are two categories of cells, one connective tissue, another amoebocytes". Müller (1956), from studies on the blood of *Lymnaea stagnalis*, concluded that amoebocytes were formed anywhere in the connective tissue, provided embryonic cells were present, and that the lung was the most prolific source.

It may be suggested that the relationships between the cell types are as follows: (1) The stellate cells and amoebocytes are perhaps interchangeable, or arise from a common embryonic cell type. (2) The Leydig's cells may originate as specialized cells by modification of stellate cells, or as a separate type derived from the embryonic cells. (3) The granule cells may arise from amoebocytes, as suggested by Kisker (1923); however, no obvious transitional forms were seen, so this suggestion is doubtful. (4) The absence of Leydig's cells may be the more primitive condition. When they first appeared in phylogeny they may have developed as specialized glycogen storage cells, and the glycogen was no longer stored in stellate cells as it appears to be in *A. trapezia*. However, these suggestions are merely tentative, and their confirmation or denial must await further studies.

V. Acknowledgments

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Appendix I

ABBREVIATIONS USED IN FIGURES 1–13

a.a.m.	anterior adductor muscle
a.p.r.m.	anterior pedal retractor muscle
ab.s.o.	abdominal sense organ
am.	amoebocyte
ao.	aorta
b.b.	brush border
b. memb.	basement membrane
b.sp.	blood space
b.v.	blood vessel
b.w.m.	muscles of body wall
c.fr.cil.	coarse frontal cilia
caec.	caecum
cil.	cilia
cil. ep.	ciliated epithelium
cil.j.	ciliary junction
ct.	ctenidium
cyt.	cyton
dig.dv.	digestive diverticula
epic.	epicuticle (periostracum)
f.	foot
f.gr.	groove on foot
fd. gr.	feeding groove
fn.fr.cil	fine frontal cilia
g.	gonopore
gl.c.	gland cell
gon.	gonad
gr.	granules
gr.c.	granule cell
gs.sh.	gastric shield
i fld.	inner fold of mantle border
i pl.	inner (medial) palp
int.	intestine
k.	kidney
k. tub.	kidney tubules
l. au.	left auricle
lat. cil.	lateral cilia
lat. o. gr.	lateral oral groove
m.fb.	muscle fibre
m.th.mt.b.	muscular thickening of the mantle border
mb.fl.	membraneous flap on outer (lateral) palp
md. fld.	middle fold of mantle border
mj.t.	major typhlosole
mn.t.	minor typhlosole
mt.	mantle
mt.r.pt.	mantle rejection point
nv.	nerve
o. fld.	outer fold of mantle border
o. pl.	outer (lateral) palp
oes.	oesophagus
p.a.m.	posterior adductor muscle
p.p.r.m.	posterior pedal retractor muscle
pig.ep.	pigmented epithelium
pl.	palp
pl.r.pt.	palp rejection point
pr.o.gr.	proximal oral groove
r.au.	right auricle
r.mt. sh.	right sheet of the mantle
rect.	rectum
ren.p.can.	renopericardial canal
s.sc.	style sac
sp.mb.ct.	suspensory membrane of ctenidium
st.	stomach
t.	typhlosole in the rectum
v.	ventricle
ves. nuc.	vesicular nucleus
y.c.	yellow cell

A STUDY OF TASMANIAN ONISCOIDEA (CRUSTACEA : ISOPODA)

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Contents

Summary

The occurrence in Tasmania of seven of the eight species of Oniscoidea previously recorded is confirmed, and additional information on the species is given. *Chiltonella tasmanica* (Chilton) is transferred to *Notoniscus* Chilton. Six known species, *Styloniscus thomsoni* (Chilton), *St. phormianus* (Chilton), *Notoniscus australis* (Chilton), *Deto marina* (Chilton), *Actaecia pallida* Nicholls & Barnes, and *Eluma caelatum* (Miers) are recorded and described from Tasmania for the first time. Ten new species are established; one of these includes specimens which formerly were wrongly assigned to *Oniscus punctatus* Thomson. The position of the genera *Styloniscus* Dana, *Notoniscus* Chilton, *Chiltonella* Vandel, *Plymophiloscia* Wahrberg, *Cubaris* Brandt, s.s. after Verhoeff, and *Sphaerillo* Verhoeff is reviewed.

A key to the families of Oniscoidea found in Tasmania is given; and, where necessary, a key to the genera in a family, or the species in a genus, is included in the section on the family or genus respectively.

I. Introduction

The earliest record of the occurrence of Oniscoidea in Tasmania was made by Haswell (1882, pp. 279, 280), who included Tasmania in the distribution of *Porcellio graniger* Miers, and a new species, *Armadillidium subdentatum*.

Budde-Lund (1885, p. 285) described a new species, *Armadillo misellus*, from a specimen collected in Tasmania.

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Three previously established species were recorded from Tasmania for the first time by Thomson (1893), who (p. 56) described *Actaecia euchroa* Dana from specimens collected at Eaglehawk Neck and (p. 54) *Oniscus punctatus* Thomson from specimens collected on Mt. Wellington, and also (p. 55) recorded *Ligia australiensis* Dana from the neighbourhood of Hobart. Chilton (1901, p. 134) realized that Thomson's specimens of *O. punctatus* from Mt. Wellington differed from those found in New Zealand, and suggested that the former should perhaps be placed in *Philoscia* Latreille. He (pp. 139, 140) recognized *Porcellio graniger* to be a synonym of *Porcellio scaber* Latreille, and noted that *P. scaber* had thus been recorded from Tasmania.

Budde-Lund (1904, pp. 87, 93) transferred *Armadillo misellus* to *Spherillo* Dana, and placed it in his own section XIII of that genus.

Chilton (1909, pp. 661–2) mentioned having an undescribed species of *Haplophthalmus* Schöbl from Tasmania, and in another paper (1911, p. 568) considered some specimens from Hobart to be *Ligia australiensis*. Subsequently (1915*a*, p. 424) he described a new species, *Haplophthalmus tasmanicus*, from a specimen collected at Fern Tree Gully, Hobart, but noted that this species differed in some characters from the definition of *Haplophthalmus* given by Sars (1899). Arcangeli (1923, p. 314) considered these differences sufficient to distinguish *H. tasmanicus* as the type of a new genus, which he named *Chiltonia*.

Jackson (1941, p. 3) proposed that *Sphaerillo* Verhoeff (non *Spherillo* Dana) should be retained as the generic name for the species included in Budde-Lund's section XIII of *Spherillo*; this implied the transference of *Spherillo misellus* to *Sphaerillo*.

The occurrence in Tasmania of "*Chiltonella tasmanica* (Chilton)" was noted by Vandel (1945, p. 236), who later (1952, p. 96) stated that Arcangeli established *Chiltonella* for *Haplophthalmus tasmanicus*. Vandel (1952, p. 30) also described a new species, *Styloniscus nichollsi*, from specimens collected at Guide River Falls, near Burnie.

In the present paper the occurrence in Tasmania of seven of the eight species previously recorded is confirmed, *Armadillidium subdentatum* Haswell being a synonym of *A. vulgare* (Latreille). The one species not represented in my collection is *Sphaerillo misellus* (Budde-Lund). Six known species are recorded and described from Tasmania for the first time. Of these, *Styloniscus thomsoni* (Chilton), *St. phormianus* (Chilton), *Notoniscus australis* (Chilton), *Deto marina* (Chilton), and *Actaecia pallida* Nicholls & Barnes occur in the mainland of Australia, New Zealand, or subantarctic islands, or in more than one of these. *Eluma caelatum* (Miers) occurs in western Europe and has probably been introduced into Tasmania. Ten species are believed to be new. One of these, *Plymophiloscia thomsoni*, sp. nov., covers the specimens which Thomson (1893) wrongly assigned to *Oniscus punctatus* Thomson, 1879.

The position of six of the genera represented, *Styloniscus* Dana, 1852, *Chiltonella* Vandel, 1952 (= *Chiltonia* Arcangeli, 1923), *Notoniscus* Chilton, 1915, *Plymophiloscia* Wahrberg, 1922, *Cubaris* Brandt, 1833, s.s. after Verhoeff, 1926,

and *Sphaerillo* Verhoeff, 1926 (non *Spherillo* Dana, 1852), is investigated. The validity of Vandel's (1952) use of the name *Styloniscus* is discussed. Confusion regarding the names *Chiltonia* Arcangeli and *Chiltonella* is pointed out, *Chiltonella* is classed as a synonym of *Notoniscus*, and the latter genus is rediagnosed accordingly. *Philoscia* (*Plymophiloscia*) *maxima* Wahrberg, 1922 is nominated as the type species of *Plymophiloscia*. Verhoeff's (1926) limits of *Plymophiloscia* are widened slightly to include species which are closest to this genus. The status of *Plymophiloscia* in relation to *Philoscia* Latreille and some of its subdivisions is considered. The position of *Cubaris*, s.s. is discussed, and an attempt is made to determine which of the species placed in *Cubaris*, s.l. may remain in *Cubaris*, s.s. The limits and synonymy of *Sphaerillo* are reviewed; *Sphaerillo pygmaeus* Verhoeff, 1926 is nominated as the type species of this genus.

II. Type Specimens

Type specimens of each of the 10 new species described are distributed as follows: A holotype male specimen and an allotype female specimen in the Australian Museum, Sydney. A paratype male specimen and a paratype female specimen in the Western Australian Museum, Perth. A paratype male specimen and a paratype female specimen in the Department of Zoology, University of Tasmania, Hobart.

With regard to previously established species, if the location of the type is not given in the section on a species, then attempts to determine this have been unsuccessful.

III. Material and Methods

Collection of specimens has been carried out mainly in the middle region of northern Tasmania, in the south-eastern part of the State, and in some areas of central Tasmania.* The material on which descriptions are based was collected by Professor V. V. Hickman, Mr. J. L. Hickman, and the author in the case of *Ligia australiensis*, *Styloniscus thomsoni*, *St. maculosus*, *St. squarrosus*, *Plymophiloscia thomsoni*, and *Cubaris hickmani*; by Mr. J. L. Hickman in the case of *Armadillidium vulgare*; and by the author in the case of the remaining species.

Specimens have been preserved in 80% alcohol. Structures examined microscopically have been mounted in "Euparal".

The descriptions of species are each based on a small number of specimens selected for detailed examination from examples of the species collected in one locality. The factors which have been taken into account in this selection are sex, largest size, most common coloration, and absence of mutilation. To avoid repetition, only one species from each genus is fully described, and the remaining species in the genus are compared with it in instances where the description given for the one species applies equally well to the same characters in another species. Length of specimens is measured along the mid-line of the body from the anterior border of the cephalon to the posterior border of the terminal segment; breadth is

* Localities referred to throughout paper are Tasmanian unless otherwise stated.

measured across the 4th segment of the pereion. Measurements of the length of structures which bear terminal processes or setae, i.e. the terminal article of the flagellum of the 2nd antenna and the rami of the uropod, do not include the length of such processes or setae.

In all cases where the sex of the animal is not specifically stated, drawings illustrate structures taken from male specimens.

IV. Key to Families of Oniscoidea Represented in Tasmania

1. Flagellum of 2nd antenna composed of more than 10 articles; male organ double ..... Ligiidae
   Flagellum of 2nd antenna composed of not more than 10 articles; male organ single 2
2. Mandible with a triturating molar process; inner lobe of 1st maxilla with 3 setose processes; male organ expanded distally ..... Styloniscidae
   Mandible with molar process represented by a tuft of setae; inner lobe of 1st maxilla with 2 setose processes; male organ not expanded distally 3
3. Littoral species; flagellum of 2nd antenna, in species found in Tasmania, composed of 4 articles; endopodite of maxilliped well developed, markedly larger than endite ..... Scyphacidae
   Inland species: flagellum of 2nd antenna composed of 3 or fewer articles; endopodite of maxilliped reduced, not markedly larger than endite 4
4. Flagellum of 2nd antenna composed of 3 articles; exopodites of all pleopods without pseudotracheae ..... Oniscidae
   Flagellum of 2nd antenna composed of 2 articles; exopodites of at least 1st and 2nd pleopods with pseudotracheae 5
5. Species found in Tasmania not able to enrol; exopodite of uropod projecting far beyond posterior border of terminal segment ..... Porcellionidae
   Species able to enrol; exopodite of uropod not, or scarcely, projecting beyond posterior border of terminal segment 6
6. Pseudotracheae present only in exopodites of 1st and 2nd pleopods; exopodite of uropod broad and laminar, occupying space between terminal segment and 5th pleuron ..... Armadillidiidae
   Pseudotracheae present in exopodites of 1st–4th or all pleopods; exopodite of uropod reduced, space between terminal segment and 5th pleuron being occupied by protopodite of uropod ..... Armadillidae

V. Family **LIGIIDAE**

Genus LIGIA Fabricius

Ligia Fabricius, 1798, p. 296.
Ligyda Rafinesque, 1814.

Type species *Oniscus oceanicus* Linnaeus, 1767.

The name *Ligia* Fabricius was predated by *Ligia* Weber, 1795, which was used for a decapod genus. However, *Ligia* Weber has been suppressed and *Ligia* Fabricius validated according to Opinion 330 of the International Commission on Zoological Nomenclature (1955).

Generic Diagnosis

A part of the definition of *Ligia* given by Sars (1899, p. 155) has been emended by Jackson (1927, p. 133) as follows:

"Body regularly oval or oblong-oval, moderately convex above, metasome confluent with mesosome or abruptly contracted. Head with occipital groove not obscured above by occiput, supra-antennal and frontal lines both present. Eyes large and convex. Antennulae small, last segment small or vestigial. Antennae strong, elongated. Mandible with a setose plume behind the lacinia mobilis and usually numerous pencilli between it and the molar process. Maxillipedes comparatively short and stout, endopodite large, five distinct or indicated segments, endite large, epipodite rounded."

The remainder of the definition, as given by Sars, was as follows:

"Legs gradually increasing in length posteriorly, dactylus distinctly bi-unguiculate. Opercular plate of uropoda sub-branchial. Uropoda more or less elongated, basal part not produced inside, rami narrow, styliform, sub-equal, each with a single apical spine."

Presumably Sars' reference to the "opercular plate of uropoda" was meant to apply to the pleopoda.

Ligia australiensis Dana

Figs. 1–14

Lygia australiensis Dana, 1853, p. 740, pl. 49, fig. 3.

Dana's brief description of *L. australiensis* was based on a mutilated specimen, collected in New South Wales. Descriptions given by Hale (1927, p. 320, 1929, p. 340) of South Australian examples which he assigned to the species, are also brief. A detailed account of my Tasmanian material is therefore given.

Male

Size.—Length of largest specimen 19 mm, breadth 8 mm.

Colour.—Live specimen yellowish green, spotted with dark brown chromatophores.

Cephalon (Fig. 1).—Maxillipedal somite distinct. Vertex indented by 2 postorbital pits. Antennary tubercles not visible in dorsal view. Eyes compound and subquadrangular, with inner border of each forming a right angle. In dorsal view, eyes separated by more than twice breadth of each eye; distance between inner angles of eyes 2·5 mm; breadth of eye from inner angle to outer edge of cephalon 0·9 mm.

First antenna (Fig. 2).—On outer side, 2nd article projects beyond base of 3rd; projection bears 3 long fine setae. There are 3 coarse setae and 1 long fine seta on dorsal surface of 3rd article.

Second antenna (Fig. 1).—When attached, antenna reaches back approximately to base of 2nd segment of pleon. Length of peduncle 9·3 mm; length of flagellum 7·5 mm. Peduncle and flagellum bear spines, each consisting of an outer sheath, split at the top into 2 points, and a central seta, clubbed at its apex. Flagellum has 20 articles, varying in length but all longer than broad.

Left mandible.—Incisor process has 4 teeth. Lacinia mobilis ends in 3 teeth, and there are 9 pencils of setae on setose lobe. Molar process triturating.

Figs. 1–14.—*Ligia australiensis* Dana: *1,* cephalon, 2nd antennae and 1st segment of pereion of male, dorsal view; *2,* distal part of left 1st antenna, dorsal view; *3,* distal part of right mandible, ventral view; *4,* distal part of outer lobe of right 1st maxilla, ventral view; *5,* distal part of left 2nd maxilla, ventral view; *6,* distal part of left maxilliped, ventral view; *7,* scale-seta on a granule on 5th tergite of pereion, dorsal view; *8,* subchelate part of left 1st leg of male, anterior view; *9,* dactylos of right 1st leg, anterior view; *10,* dactylos of left 7th leg, anterior view; *11,* male organs, dorsal view; *12,* terminal segment, dorsal view; *13,* left 2nd pleopod of male, ventral view (blood vessels in exopodite not shown); *14,* exopodite of left 3rd pleopod of male, ventral view.

Right mandible (Fig. 3).—Apical border of lacinia mobilis serrated on ventral side; on dorsal side it is produced into a blunt point. In other respects right mandible is similar to left.

First maxilla.—Outer lobe (Fig. 4) ends in 11 teeth and 2 setose processes. Of the 6 smaller inner teeth, outermost and innermost are simple, the rest have small lateral points. Outer setose process slender and feathery, inner one broader. Apex of inner lobe not marked off by a suture from remainder of lobe. Inner lobe bears 3 setose processes.

Second maxilla (Fig. 5).—Division into 2 lobes indicated by an indentation in distal margin of maxilla and a suture line on ventral surface. Outer lobe bears fine setae. Most of setae on inner lobe directed inwards, but on dorsal surface there is a conspicuous oblique band of upright setae. On inner side of inner lobe there is a brush of long simple setae, but no setose processes present. There is a U-shaped band of chitin on dorsal surface of inner lobe.

Maxilliped (Fig. 6).—Ischion and dactylos distinct; divisions separating meros, carpos, and propodos distinct on inner side, but towards outer side of endopodite these articles are delimited from each other only by suture lines on ventral surface. There are 2 spines on outer border. Spiny setae occur on inner border of meros, carpos, and propodos, and on apex of dactylos. Endite subquadrangular with outer border curved outwards; its apex and inner surface setose. There are 2 spines on dorsal surface near apex; near inner spine is a small setose process.

Pereion.—Epimera of 1st and 2nd segments nearly transverse with posterior angles right-angled; epimera of 3rd-7th segments slope backwards with posterior angles subacute. Coxal grooves not evident. Dorsal surface finely granulate. Each granule bears a scale-seta (Fig. 7) having a long narrow scale portion and a seta clubbed at its apex. Broad strongly chitinized scales cover base of scale-seta. Between granules, tergites have covering of small simple scales. Scale-setae present along lateral borders of segments.

Pereiopods.—Carpos of first leg expanded and oval; propodos and dactylos bent under it to form a subchelate hand (Fig. 8). Opposing faces of carpos and propodos striated; under surfaces of these articles indented. No distinctive process on propodos. Spines on leg formed like those on 2nd antenna. Dactylos (Fig. 9) has terminal claw and accessory claw. Dactylar seta long and uniformly narrow, not clubbed at apex.

Second and 3rd legs also subchelate, but in 3rd leg carpos is less expanded than in 1st leg. Fourth to 7th legs not subchelate; carpos in these legs subcylindrical. Second to 5th legs each have a single dactylar seta as in 1st leg. On 6th and 7th legs a group of numerous such long narrow setae is on upper surface of dactylos. Dactylos of 7th leg shown in Figure 10.

Male organs (Fig. 11).—Two long narrow structures, fused at the base and extending backwards almost to posterior angles of exopodites of 5th pleopods. Apices of organs bluntly rounded and curved inwards, exhibiting areas of fine setae. On dorsal surface, towards base of each organ, is a curved band of chitin.

This continues as a narrow ridge which extends down middle third of organ and is ornamented along its outer side with small oblique strips of chitin. Towards inner side, another ridge runs parallel to first ridge and extends beyond it distally; this second ridge bears fine setae. A ridge on ventral surface of organ is not ornamented.

Pleon.—Not abruptly narrower than pereion. Pleura of 3rd–5th segments large, acute, and directed backwards. Terminal segment (Fig. 12): Posterolateral angles subacute, not extending back as far as does centre of segment. Outer accessory processes absent, inner accessory processes bluntly rounded. Posterior border between inner accessory processes forms a very obtuse median angle. Jackson (1922, p. 686) recognized among species of *Ligia* two main types of terminal segment, "triangulate", in which this border has a median process, and "arcuate", in which it is evenly rounded. The terminal segment of *L. australiensis* may be classed as triangulate, but the angle is so obtuse that it very nearly approaches the arcuate type. Dorsal surface of pleon finely granulate. Arrangement of scales and scale-setae similar to that on pereion.

First pleopod.—Exopodite suboval, fringed with plumose setae; it encloses conspicuous blood vessels. Endopodite branchial, not sexually differentiated.

Second pleopod (Fig. 13).—Exopodite subquadrangular, fringed with plumose setae. Blood vessels occur in exopodite but they are omitted from Figure 13 so that the underlying portion of the endopodite may be more clearly shown. Length of articles of endopodite: 1st 1·12 mm, 2nd 5·10 mm. Second article tapers to an acute apex which is permanently twisted; apical region exhibits very fine setae. There is a wide groove down ventral surface of article, outer wall of which, along its middle third, is set with blunt spines. Beyond this, article twists and groove opens on outer side of endopodite. When in position on animal, male organ fits into groove in 2nd article. Where groove opens outwards, endopodite twists to inner side of male organ, across its ventral surface, and finally the apical point curves round outer side of apex of male organ.

Third pleopod.—Exopodite (Fig. 14) subquadrangular, fringed with plumose setae. The pattern of blood vessels varies in small details in different exopodites, but that shown in Figure 14 represents their general arrangement in the 3rd pleopod and is similar to that found in exopodites of all other pleopods.

Uropod.—Protopodite subcylindrical with inner surface convex, outer angle prolonged slightly beyond base of exopodite. Rami styliform. Length of articles: protopodite 2·3 mm, exopodite 3·4 mm, endopodite 3·7 mm. Maximum breadth of protopodite 1·0 mm.

Female

Length of largest specimen 18 mm, breadth 8 mm. Female differs from male in the following structures:

Second antenna.—When attached, 2nd antenna reaches back approximately to base of 7th segment of pereion. Length of peduncle 7·5 mm; length of flagellum 6·6 mm.

Pereiopods.—First to 3rd legs not subchelate but of same form as remaining legs.

Second pleopod.—Endopodite subtriangular and branchial.

Uropod.—Proportions of lengths of articles, relative to each other and to length of body, are different; length of protopodite 1·9 mm, of exopodite 2·7 mm, of endopodite 2·8 mm. Maximum breadth of protopodite 0·9 mm.

Habitat

Description is based on specimens found under stones and seaweed near high-tide level on a rocky shore at Pirates' Bay, Eaglehawk Neck, on 19.iv.1956; 72 males and 131 females obtained. Other specimens were found under similar conditions at Ulverstone, Devonport, Hawley, Low Head (East Tamar), South Arm, Tinderbox and Adventure Bay, Bruny I. Examples were also found under stones and debris on the shore of the Tamar R. at Sandy Beach and Gravelly Beach, and the Derwent R. at Hobart and East Risdon, but the animals were not as numerous along these estuaries as on the nearby sea-coast at Low Head and Eaglehawk Neck respectively.

Variation

Number of articles in flagellum of 2nd antenna in my specimens from Eaglehawk Neck varies from 18 to 22, although the most common number is 20.

Remarks

As my Tasmanian specimens of *Ligia* agree with the original description of *L. australiensis*, I assign them to this species. However, Dana's description is a brief one which was based on a mutilated specimen. Consequently the position of *L. australiensis* has been regarded by some authors as uncertain. Jackson (1922, p. 701) included *L. australiensis* in a list of species of *Ligia* which were insufficiently described or of doubtful validity. Vandel (1945, p. 229) preceded this species with a question mark.

Reference to Jackson's (1922) descriptions of adequately known species in his revision of *Ligia*, and to descriptions of species of *Ligia* in the following later works: Verhoeff (1926), Edmondson (1931), Barnard (1932), Jackson (1933*b*, 1938), Van Name (1936), Collinge (1946), Vandel (1948), indicates that *L. australiensis* has the most characters in common with *L. novae-zealandiae* Dana, 1853. However Chilton (1911, p. 568) stated that specimens from Victoria and Hobart, which he considered to be *L. australiensis*, differed from *L. novae-zealandiae* in a few details in the appendages. A comparison of characters of my specimens of *L. australiensis* from Eaglehawk Neck with those of *L. novae-zealandiae*, as described and figured by Chilton (1901, p. 107), confirms that differences between the species do occur (see tabulation below). The position of *L. australiensis* as a valid species is therefore upheld.

Ligia australiensis	*Ligia novae-zealandiae*
Second maxilla with division into 2 lobes indicated by a suture line	Second maxilla with no indication of division into 2 lobes
First to 5th legs each with a single dactylar seta, uniform in width; 6th and 7th legs with many such setae on dactylos	First to 7th legs each with a single dactylar seta, clubbed at the end
Male organs curved inwards at the end, with apices bluntly rounded	Male organs curved outwards at the end, with apices acute
Pleon not abruptly narrower than pereion	Pleon abruptly narrower than pereion
Posterior border of terminal segment produced into a very obtuse median angle	Posterior border of terminal segment evenly curved in the centre
Distal region of endopodite of 2nd male pleopod permanently twisted	Endopodite of 2nd male pleopod not twisted

Chilton described and figured the male organs of *L. novae-zealandiae* as adherent to the 1st pleopods and grooved on the dorsal surface. If this is so, *L. australiensis* also differs from *L. novae-zealandiae* in this regard. However, Barnard (1932, p. 185) queried these observations of Chilton's.

Verhoeff (1926, p. 347) divided *Ligia* Fabricius into five genera, and denoted *L. novae-zealandiae*, which he attributed to Chilton instead of Dana, as the type species of one of his new genera, *Nesoligia*. Use of Verhoeff's key to these genera indicates that *L. australiensis* can also be included in *Nesoligia*. However, Verhoeff's subdivisions were criticized by Jackson (1938, p. 175). *Nesoligia* was regarded as a subgenus of *Ligia* Fabricius by Van Name (1936) and Jackson (1941). I therefore retain *L. australiensis* in *Ligia* Fabricius.

Hale (1927, p. 320), in describing a male specimen of *L. australiensis* from Kangaroo I., S. Aust., stated that the 2nd antennae were distinctly longer than the body, exclusive of the uropods. In my Tasmanian specimens the 2nd antennae of both sexes are shorter than the body.

Barnard (1932, p. 186) referred to a South Australian species of *Ligia* which he considered distinct from *L. novae-zealandiae*. This species may well have been *L. australiensis*; its male organs, which Barnard (fig. 1*c*) figured in outline, were the same shape as those of *L. australiensis*.

VI. Family **STYLONISCIDAE**

Key to Genera of Styloniscidae Represented in Tasmania

Pereion without tubercles or with tubercles not arranged in longitudinal rows; 3rd–5th pleura small and adpressed ..... *Styloniscus*

Pereion with tubercles arranged in longitudinal rows; 3rd–5th, or 4th and 5th, pleura large and expanded laterally ..... *Notoniscus*

Genus STYLONISCUS Dana

Styloniscus Dana, 1852, p. 302.
Megatrichoniscus Jackson, 1938, p. 176 (non Brian, 1921)
Patagoniscus Verhoeff, 1939, p. 305.
Antarctoniscus Paulian de Félice, 1940, p. 307.
?*Oligoniscus* Dollfus, 1890*b*, p. 71.

Type species *Styloniscus magellanicus* Dana, 1853.

Dana (1852) defined a new genus, *Styloniscus,* including it in his new subfamily, Scyphacinae, of family Oniscidae, and in another paper (1853) he placed in it two new species, *St. magellanicus* (p. 736) from Tierra del Fuego, S. America, and *St. longistylis* (p. 737) from Tongatabu, Friendly Is. (Tonga). Dana (1854, p. 176) later established a third species, *St. gracilis,* from California.

Sars (1899, p. 155) included *Styloniscus* in family Ligiidae. Stebbing (1900*a*, p. 564) believed *St. magellanicus* and *St. longistylis* to be generically distinct. On the evidence of Dana's description he transferred *St. magellanicus* to *Trichoniscus* Brandt, 1833 in family Trichoniscidae, and (p. 566) described specimens from the Falkland Is. under the name *Trichoniscus magellanicus* (Dana). Stebbing retained *St. longistylis* and *St. gracilis* in *Styloniscus,* which he considered might still belong in the Ligiidae. Richardson (1905, p. 690) transferred *St. gracilis* to *Ligidium* Brandt, 1833. Budde-Lund (1906, p. 83) ranked *Styloniscus* as a subgenus of *Trichoniscus,* and retained in it *Tr.* (*St.*) *magellanicus.* He (p. 84) considered that *St. longistylis* probably might be a *Spherillo.*

Jackson (1938, p. 176) included *Tr. magellanicus* in *Megatrichoniscus,* a new subgenus of *Trichoniscus.* (This name was preoccupied by *Megatrichoniscus* Brian, 1921). Verhoeff (1939) realized that *Tr. magellanicus* did not even belong in the Trichoniscidae and included it in a new family, Patagoniscidae, and new genus, *Patagoniscus.* Jackson (1941, p. 7) designated *St. longistylis,* the only species then remaining in the genus, as the type species of *Styloniscus,* which he included in the family Ligiidae. In this paper his earlier procedure of placing *Tr. magellanicus* in *Trichoniscus* (*Megatrichoniscus*) was followed, no reference being made to Verhoeff's (1939) paper. Vandel (1952, p. 14) recognized that *Styloniscus* had priority over *Patagoniscus.* He placed *Styloniscus* in a new family, Styloniscidae, maintaining (p. 94) that the family which has as its type the genus *Styloniscus* should bear the name Styloniscidae; also he (p. 15) considered that Verhoeff's Patagoniscidae was not solidly established. Vandel (p. 14) quoted *St. magellanicus* as the type species of *Styloniscus,* and stated that the position of *St. longistylis* remained obscure. Vandel noted Jackson's (1941) reference to this species but did not discuss his designation of *St. longistylis* as the type of *Styloniscus.*

On p. 18, Vandel claimed that the isopods from the Falkland Is. described by Stebbing (1900*a*) under the name *Trichoniscus magellanicus* corresponded in fact to *Deto marina* (Chilton), but Stebbing described his specimens as having eyes with 3 visual elements, flagellum of 2nd antennae with 7–8 articles, mandibles with a molar process, and inner lobe of 1st maxillae with 3 plumose setae. These characters do not agree with those of *Deto marina,* but they are consistent with those of a species of *Styloniscus.* As the Falkland Is. are situated in the vicinity of the type locality of Tierra del Fuego, it seems reasonable to assume that Stebbing's specimens did indeed belong to *St. magellanicus.*

Jackson (1941) appears to have been the first author to designate a type species for *Styloniscus.* Therefore Vandel's later naming of *St. magellanicus* as the type species seems to be a contravention of Article 30 of the Rules of Zoological

Nomenclature (cf. Section II(*g*) in Schenk and McMasters (1936, p. 35)) which states that if an author, in publishing a genus with more than one valid species, fails to designate or indicate its type, any subsequent author may select the type, and such designation is not subject to change. It should be noted that Jackson's designation of *St. longistylis* as type was probably due to the fact that in 1941 this was the only species of *Styloniscus* which had not been placed in another genus (type by elimination; see Section III(*k*) in Schenk and McMasters (1936, p. 35)). But the identity of *St. longistylis* is very uncertain. Dana's description indicates that this species probably belongs to the Ligiidae, but it is not sufficient to confirm this. To my knowledge, the species has not been recorded again, nor has the original material been redescribed. On the other hand, *St. magellanicus* has been recorded and described by other authors since Dana. The material examined by Vandel included specimens from Natales, Chile, which is situated on the mainland adjacent to the type locality of Tierra del Fuego. Vandel's study of members of the trichoniscid group from the southern hemisphere is of value in determining the systematic position of these isopods, and the genus *Styloniscus*, as he defined it, includes an assemblage of closely related species. Thus, although it would appear correct to follow Jackson in regarding *St. longistylis* as the type of *Styloniscus*, and so to rename the genus based on *St. magellanicus* as type, in my opinion this procedure would only cause further confusion. Therefore, in the present paper, I propose to follow Vandel in using the name *Styloniscus* for the genus whose type is *St. magellanicus*.

Generic Diagnosis

The following generic diagnosis has been translated from the original French as given by Vandel (1952, p. 15):

"(1) Size often large (up to 14 mm); but some species are of small size (for example *phormianus* Chilton, *mauritianus* Barnard, *affinis* n.sp.).

(2) Ocular apparatus formed of three clearly separated ommatidia (according to Verhoeff, certain species possess a single ommatidium).

(3) Cephalon of normal trichoniscian type.

(4) Right mandible with one, left mandible with two pencils. The right mandible bears a molar pencil in all the species (studied by me), with the exception of *mauritiensis* (subgenus *Indoniscus*).

(5) Genital apophysis enlarged at its extremity, and terminated by a small, conical process.

(6) First male pleopod: protopodite very elongated in the transverse sense; exopodite simple, without a stalk; endopodite cylindrical, terminated by a long stalk, not setose, immobile (because deprived of muscles). The extensor and flexor muscles of the appendage are extremely long and strong and are inserted at the base of the endopodite; they are supported by an apodeme detached from the sternite."

In paragraph (1) of this diagnosis, the name *mauritiensis* Barnard has been misspelled as *mauritianus*; also Vandel has mentioned *affinis* n.sp., but no species of this name was described in his paper.

Vandel (1952, p. 16) placed definitely in *Styloniscus* the following eight species of which he examined specimens: *St. magellanicus* Dana, 1853, *St. thomsoni*

(Chilton, 1885), *St. phormianus* (Chilton, 1901), *St. otakensis* (Chilton, 1901), *St. spinosus* (Patience, 1907), *St. tabulae* (Barnard, 1932), *St. mauritiensis* (Barnard, 1936) and *St. nicholsi* Vandel, 1952. He considered that, according to the descriptions and figures given by their authors, the following 19 species very probably belong in *Styloniscus*: *Trichoniscus verrucosus* Budde-Lund, 1906; *Tr. hottentoti, Tr. natalensis, Tr. ventosus, Tr. capensis, Tr. moruliceps, Tr. austro-africanus, Tr. georgensis, Tr. horae, Tr. cestus, Tr. swellendami, Tr. riversdalei,* all Barnard, 1932; *Patagoniscus nordenskiöldi, P. pallidus, P. araucanicus, P. simrothi, P. iheringi, P. schwabei,* all Verhoeff, 1939; *Tr.* (*Antarctoniscus*) *jeanneli* Paulian de Félice, 1940. Verhoeff (1939) indicated that *P. nordenskiöldi, P. pallidus,* and *P. iheringi* were already established in a paper which was being published in Stockholm, but this paper did not appear until 1951. Vandel stated that the following four species possibly belong in *Styloniscus*: *Tr. australis* Dollfus, 1890, *Tr. murrayi* Dollfus, 1890, *Oligoniscus monocellatus* (Dollfus, 1890), *Tr. kermadecensis* Chilton, 1911. He believed that *Tr. commensalis* Chilton, 1910, probably represents the type of a special genus. However, I suggest that if *Tr. kermadecensis* is to be considered as possibly belonging in *Styloniscus* then *Tr. commensalis,* which has characters in common with this species, e.g. pleon not abruptly narrower than pereion, should also be considered here. *St. longistylis* Dana probably does not belong in *Styloniscus* as defined by Vandel; its position has already been discussed.

Thus altogether there are 32 established species which appear to belong in *Styloniscus*. Reference to descriptions given by Vandel (1952) and by the original authors of the species indicates that two of the five species of *Styloniscus* which I have collected cannot be identified with any of these. Due to the brevity of some accounts, it is not possible to demonstrate the distinction of the two new species from all of the established species by means of a single key. Consequently the species described by Verhoeff (1939, 1951) are omitted from the following key and considered separately in a later key. A key to species of *Styloniscus* represented in Tasmania is also given below.

KEY TO SPECIES OF THE GENUS STYLONISCUS (EXCLUDING VERHOEFF'S SPECIES)

1. Eye composed of 1 ocellus ..... *monocellatus*
   Eye composed of 3 ocelli 2
2. Pereion smooth 3
   Pereion tuberculate or uneven 6
3. Ocelli of eye contiguous, or arranged in a line, or both ..... *tabulae, mauritiensis, hottentoti, natalensis, austro-africanus*
   Ocelli of eye separated and arranged in a triangle 4
4. Flagelliform process of endopodite of 1st male pleopod lacking setae ..... *magellanicus, phormianus*
   Flagelliform process of endopodite of 1st male pleopod bearing setae 5
5. Ischion of 7th leg without sexual differentiation ..... *thomsoni*
   Ischion of 7th leg showing sexual differentiation ..... *maculosus,* sp. nov.
6. Pleon not abruptly narrower than pereion ..... *commensalis, kermadecensis*
   Pleon abruptly narrower than pereion 7

7. Pleon with dorsal surface of all or majority of its segments tuberculate or uneven .... *otakensis, spinosus, nichollsi, georgensis, swellendami, riversdalei, jeanneli, murrayi, australis*
Pleon with dorsal surface of all segments, or all but 3rd segment, smooth 8
8. Ocelli of eye contiguous, or arranged in a line, or both .... *ventosus, capensis, moruliceps, horae, cestus*
Ocelli of eye separated and arranged in a triangle 9
9. Dorsal surface of 3rd segment of pleon smooth ..... *verrucosus*
Dorsal surface of 3rd segment of pleon with a row of tubercles .... *squarrosus*, sp. nov.

KEY TO SPECIES OF THE GENUS STYLONISCUS DESCRIBED BY VERHOEFF (1939, 1951), AND NEW SPECIES

1. Eye composed of 1 ocellus ..... *araucanicus, schwabei*
Eye composed of 3 ocelli 2
2. Terminal process of male organ in form of a blunt knob .... *pallidus, iheringi, simrothi*
Terminal process of male organ in form of a cone 3
3. Exopodite of 1st male pleopod with its outer border not indented .. *maculosus*, sp. nov.
Exopodite of 1st male pleopod with its outer border indented 4
4. Ischion of 7th leg of male with its under surface incurved; terminal process of male organ provided with small teeth ..... *nordenskiöldi*
Ischion of 7th leg of male with its under surface not incurved, so that its lower border is straight; terminal process of male organ without teeth ..... *squarrosus*, sp. nov.

KEY TO SPECIES OF THE GENUS STYLONISCUS REPRESENTED IN TASMANIA

1. Second article of endopodite of 2nd male pleopod with inner side curved in abruptly at about one-quarter of its length from apex, so that its apical point is asymmetrical, continuous with outer half of endopodite ..... *nichollsi*
Second article of endopodite of 2nd male pleopod with inner side not curved in abruptly at a distance from apex; apical point almost symmetrical with remainder of endopodite 2
2 Cephalon and pereion with transverse rows of tubercles ..... *squarrosus*, sp. nov.
Cephalon and pereion not tuberculate 3
3. Cephalon and pereion set with numerous large setae; flagelliform process of endopodite of 1st male pleopod lacking setae ..... *phormianus*
Cephalon and pereion with few or no setae; flagelliform process of endopodite of 1st male pleopod bearing setae 4
4. Ischion of 7th leg without sexual differentiation; flagelliform process of endopodite of 1st male pleopod having setae restricted to a tuft at apex and lacking setose pencils ..... *thomsoni*
Ischion of 7th leg showing sexual differentiation; flagelliform process of endopodite of 1st male pleopod having its distal quarter setose and bearing 3 setose pencils at apex ..... *maculosus*, sp. nov.

STYLONISCUS THOMSONI (Chilton)

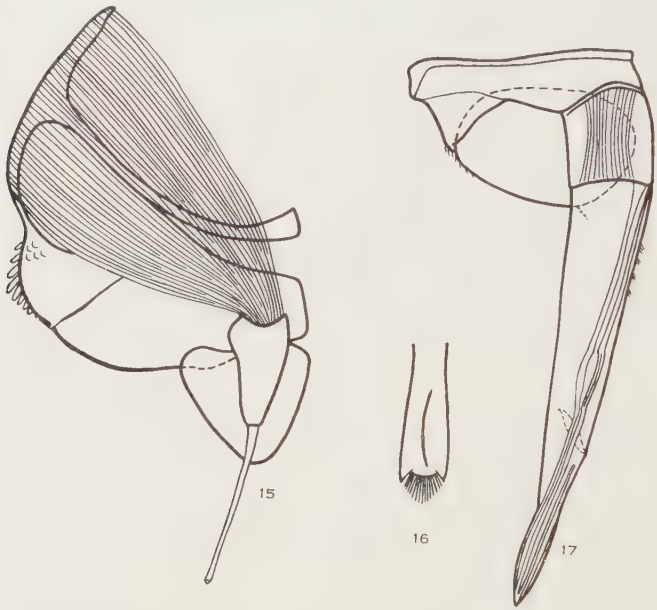
Figs. 15–17

Philougria Thomsoni Chilton, 1885, p. 576.
Philygria Thomsoni Chilton, 1886, p. 159, pl. 5, figs. 1–6.
Trichoniscus Thomsoni Chilton, 1901, p. 118, pl. 13, fig. 1.
Trichoniscus (Megatrichoniscus) thomsoni Jackson, 1938, p. 176, fig. 3.
Patagoniscus thomsoni Verhoeff, 1939, p. 304.
Styloniscus thomsoni Vandel, 1952, p. 36, figs. 29–34.

Location of type specimen.—Syntype material on two slides is at present located in the Department of Zoology, University of Canterbury, Christchurch, N.Z. These slides will subsequently be transferred to the Canterbury Museum, Christchurch.

Distinguishing Characters

Size.—Length of largest male specimen 6·0 mm, breadth 2·7 mm; length of largest female specimen 6·4 mm, breadth 3·2 mm.



Figs. 15–17.—*Styloniscus thomsoni* (Chilton): *15,* left 1st pleopod of male, dorsal view; *16,* distal part of endopodite of left 1st pleopod of male, dorsal view; *17,* left 2nd pleopod of male, dorsal view.

Body.—Background colour of live animal light brown marked with patches of dark brown, or orange with dark brown patches, or red with dark markings almost black. Unpigmented patches not conspicuous in live animal. Surface of body smooth. Eyes each composed of 3 large ocelli, very widely separated from one another and arranged in a triangle. Terminal segment trapezoidal with posterior border straight.

First male pleopod (Fig. 15).—Exopodite subtriangular with outer border not indented. Flagelliform process of endopodite bears at its apex (Fig. 16) a wide tuft of setae; no other setae on process apart from apical tuft.

Second male pleopod (Fig. 17).—Length of articles of endopodite: 1st 0·25 mm, 2nd 1·05 mm. Second article tapers to a narrow point, scarcely bent outwards. On ventral surface, an oblique chitinous thickening is situated at about two-fifths of length of article behind apex. Half-way between this thickening and

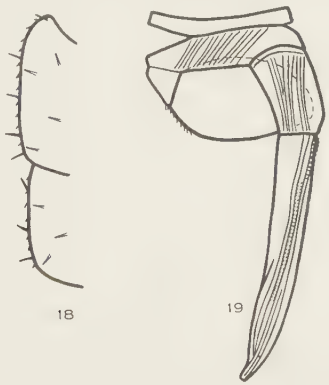
apex is a constriction in width of endopodite. On dorsal surface a groove extends obliquely down length of article. In apical region are several longitudinal ridges of chitin.

Fifth male pleopod.—Groove for endopodite of 2nd pleopod extends down whole length of exopodite.

Second female pleopod.—Length of exopodite approximately two-thirds that of endopodite; lengths (along inner border): exopodite 0·40 mm, endopodite 0·62 mm.

Habitat

Description is based on specimens found in debris and under wood on the ground at altitudes of 1900–3900 ft on Mt. Wellington; collections made were as follows: 15.v.1956, 2 males, 9 females; 22.x.1956, 3 males, 9 females; 6.iii.1957, 8 males, 11 females; 28.v.1957, 12 males, 42 females. Specimens were also found in decaying wood and forest debris at Collinsvale and Tarraleah, and in Mt. Field National Park and the Florentine Valley.



Figs. 18 and 19.—*Styloniscus phormianus* (Chilton): *18*, left epimera of 1st and 2nd segments of percion, dorsal view; *19*, left 2nd pleopod of male, dorsal view.

Styloniscus phormianus (Chilton)

Figs. 18, 19

Philougria rosea Chilton, 1883, p. 73 (in part), non Koch, 1835–44.
Philygria rosea Thomson and Chilton, 1886, p. 157 (in part).
Trichoniscus phormianus Chilton, 1901, p. 115, pl. 12, fig. 1.
Patagoniscus phormianus Verhoeff, 1939, p. 303.
Styloniscus phormianus Vandel, 1952, p. 47, figs. 40–44.

Distinguishing Characters

Size.—Length of largest male specimen (collected at Collinsvale) 2·0 mm, breadth 0·9 mm; length of largest female specimen (collected at Collinsvale) 2·5 mm, breadth 1·2 mm.

Body.—Dorsal surface of live specimen purplish brown marked with conspicuous unpigmented patches. A pigmented band extends down centre of

pereion. Surface of body smooth. Cephalon and pereion bear large scattered setae (see Fig. 18). Eyes each composed of 3 ocelli, separated from each other and arranged in a triangle. Terminal segment trapezoidal with posterior angles slightly rounded.

First male pleopod.—Exopodite subtriangular with outer border indented, apex slightly bent outwards. Flagelliform process of endopodite simply pointed at apex and lacking setae.

Second male pleopod (Fig. 19).—Length of articles of endopodite: 1st 0·10 mm, 2nd 0·33 mm. Width of 2nd article almost uniform until just before apex, where it narrows to a blunt point which is slightly bent outwards. On dorsal surface a groove extends obliquely down length of article. In middle third, walls of groove exhibit backwardly sloping chitinous ridges. At base of article, inner wall of groove set with a row of blunt setose processes.

Fifth male pleopod.—Groove for endopodite of 2nd pleopod occupies approximately half length of exopodite.

Second female pleopod.—Length of exopodite approximately three-fifths that of endopodite; lengths (along inner border): exopodite 0·14 mm, endopodite 0·23 mm.

Habitat

Description is based on specimens found in debris on the ground in a myrtle forest at Collinsvale, on 19.vi.1957; 5 males and 13 females obtained. Other specimens were found in forest debris at Fern Tree and also higher up on Mt. Wellington at an altitude of about 1900 ft, and at Tarraleah.

Remarks

The pereiopods of the New Zealand specimens of *St. phormianus* described by Chilton (1901, p. 115) and Vandel (1952, p. 47) did not exhibit sexual differentiation. In the specimens from Collinsvale there are hyaline scales on the under surface of meros and carpos of the 1st and 2nd legs of the male, but such scales are not present on the corresponding legs in the female.

On 7.x.1957, 15 males and 19 females were collected from debris lying on the ground in a forest of eucalypts and tree ferns at Tarraleah. These specimens are considerably larger than those found at Collinsvale and on Mt. Wellington, and 4 of the males and 11 of the females are more extensively pigmented. Measurements of largest male specimen from Tarraleah are: length 4·8 mm, breadth 2·4 mm; those of largest female specimen are: length 7·2 mm, breadth 3·6 mm.

Chilton (p. 116) gave the size of his specimens as "about 4 mm". Vandel (p. 49) stated the length of his specimens to be 2 mm. None of the female specimens from Collinsvale is carrying embryos, but among specimens from Mt. Wellington are three ovigerous females, one 2·1 mm long and the other two each 2 mm long. It is therefore likely that the specimens from Collinsvale are at least mature, even if not fully grown. However, as I could find no morphological distinction between the large specimens from Tarraleah and the small specimens from Collinsvale, I have assigned the former also to *St. phormianus*.

Styloniscus nichollsi Vandel

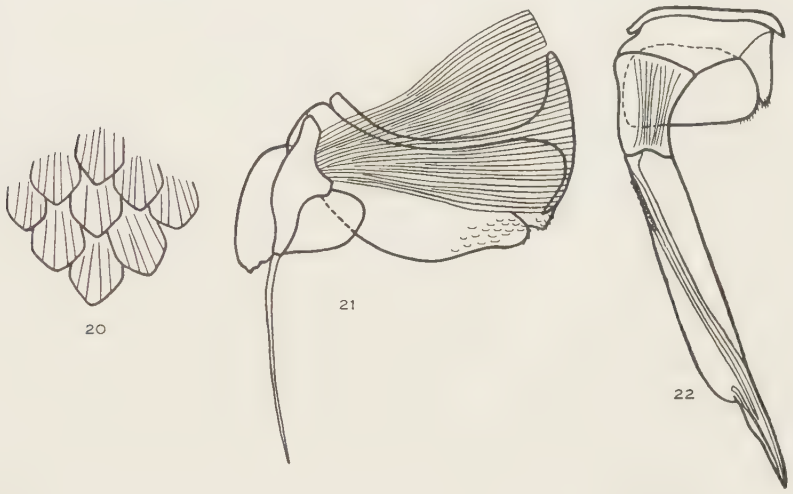
Figs. 20–22

Styloniscus nichollsi Vandel, 1952, p. 30, figs. 21–28.

Location of type specimens.—Type specimens are in the possession of the author, Professor A. Vandel, Faculté des Sciences, Toulouse, France, who intends eventually to deposit them in the Muséum National d'Histoire Naturelle, Paris.

Distinguishing Characters

Size.—Length of largest male specimen 3·1 mm, breadth 1·5 mm; length of largest female specimen 4·6 mm, breadth 2·3 mm.



Figs. 20–22.—*Styloniscus nichollsi* Vandel: *20,* scales on dorsal surface of 7th segment of pereion, dorsal view; *21,* right 1st pleopod of male, dorsal view; *22,* right 2nd pleopod of male, dorsal view.

Body.—Dorsal surface of live animal dark brown, marked with conspicuous unpigmented patches. Surface of body slightly roughened but not conspicuously tuberculate. Eyes each composed of 3 ocelli, separated from each other and arranged in a triangle. Terminal segment trapezoidal with posterior border straight.

First male pleopod (Fig. 21).—Exopodite subtriangular with outer border indented and apex slightly crenate. Flagelliform process of endopodite simply pointed at apex and lacking setae.

Second male pleopod (Fig. 22).—Length of articles of endopodite: 1st 0·18 mm, 2nd 0·63 mm. Inner side of 2nd article curves inwards abruptly at about one-quarter of its length from apex, so that apical point is asymmetrical, continuous with outer half of endopodite. A groove extends down dorsal surface of 2nd article. Near base of article, inner border of groove exhibits blunt tooth-like processes.

Fifth male pleopod.—Groove for endopodite of 2nd pleopod extends down whole length of exopodite.

Second female pleopod.—Length of exopodite approximately half that of endopodite; lengths (along inner border): exopodite 0·22 mm, endopodite 0·43 mm.

Habitat

Description is based on specimens found in debris on the ground at an altitude of about 1900 ft on Mt. Wellington, on 26.vi.1957; 8 males and 11 females obtained. Other specimens were found in grass tussocks on Queen's Domain, Hobart, under stones in the University Park, Sandy Bay, Hobart, in forest debris in Mt. Field National Park and at Tarraleah, and under pieces of wood lying on the ground near a beach at West Ulverstone.

Vandel's specimens were collected in mosses along a stream at Guide River Falls, 10 miles from Burnie.

Variations

My specimens from Sandy Bay are a lighter and more reddish brown than those from Mt. Wellington.

The small elevations on dorsal surface of cephalon and pereion of the specimens from West Ulverstone are more pronounced than those of the specimens from Mt. Wellington; cephalon and pereion of the former thus appear finely granulate.

Remarks

Vandel (p. 32, fig. 24, C) described and figured the outer lobe of the 1st maxilla as having 10 teeth and 2 setose processes. In specimens from Mt. Wellington this structure has 11 teeth and 2 setose processes. Vandel (p. 30) stated that scales on the carapace of his specimens were not striated, and (p. 31) indicated that scale-setae were absent from the 3rd to 7th pereial tergites. In specimens from Mt. Wellington, scale-setae occur on all pereial tergites, and striations are apparent on the scales which cover the dorsal surface of the pereion (see Fig. 20). However, due to the agreement of other characters, especially those of the 1st and 2nd male pleopods, of my specimens with those of Vandel's specimens, I have no hesitation in assigning my examples to *St. nichollsi*.

Styloniscus maculosus, sp. nov.

Figs. 23–41

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

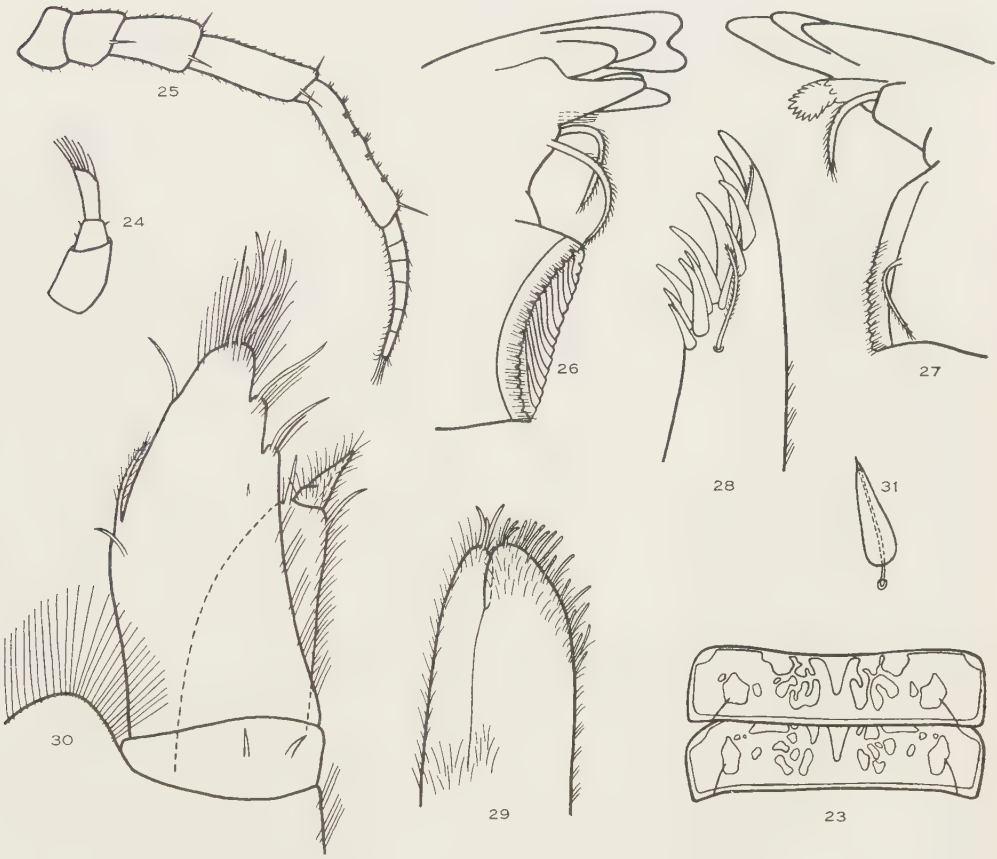
Male

Size.—Length of largest specimen 4·90 mm, breadth 2·25 mm.

Colour.—Dorsal surface of live animal dark brown marked with conspicuous unpigmented patches. On all pereial tergites there is a large unpigmented patch on each side near base of epimeron, with an area of smaller patches between this and centre of tergite. A V-shaped unpigmented patch occurs in mid-line on

anterior region of 2nd–7th pereial tergites and 1st tergite of pleon. These patches together form a conspicuous row down mid-line, while patches at base of epimera form a similar row on each side. Distribution of unpigmented areas on 4th and 5th pereial tergites shown in Figure 23.

Cephalon.—Surface of vertex smooth. Frontal line absent; supra-antennal line present. Antennary tubercles obtuse-angled. Eyes each composed of 3 ocelli, separated from each other and arranged in a triangle.



Figs. 23–31.—*Styloniscus maculosus,* sp. nov.: *23,* fourth and 5th tergites of pereion, showing distribution of unpigmented areas; *24,* right 1st antenna, ventral view; *25,* left 2nd antenna, ventral view; *26,* distal part of left mandible, dorsal view; *27,* distal part of right mandible, dorsal view; *28,* distal part of outer lobe of left 1st maxilla, ventral view; *29,* distal part of right 2nd maxilla, ventral view; *30,* distal part of right maxilliped, ventral view; *31,* scale-seta on lateral border of 1st segment of pereion, dorsal view.

First antenna (Fig. 24).—Third article spatulate with 6 long setae on apical border and 1 seta on inner border.

Second antenna (Fig. 25).—Length of peduncle 1·78 mm; length of flagellum 0·60 mm. Anterior surface of 5th article undulating, bearing groups of hyaline

scale-setae which form 2 series, a dorsal row of 5 groups and a ventral row of 4 groups. Flagellum has 6 articles.

Left mandible (Fig. 26).—Incisor process consists of a bifid tooth and 2 simple teeth. Lacinia mobilis ends in 3 teeth; at its base are a tuft of simple setae and 2 pencils of setae. Molar process triturating; no molar pencil.

Right mandible (Fig. 27).—Incisor process consists of 3 simple teeth. Lacinia mobilis club-shaped with a ring of tooth-like processes at apex; 1 pencil of setae behind its base. There is a pencil of setae on molar process.

First maxilla.—Outer lobe (Fig. 28) ends in 11 simple teeth and 2 slender processes; latter are set at an angle to long axis of lobe and their distal ends bear short setae. Inner lobe bears 3 setose processes.

Second maxilla (Fig. 29).—Apical region divided into 2 rounded lobes. Outer lobe bears 3 spines and a fringe of fine setae. Inner lobe bears coarse and fine setae.

Maxilliped (Fig. 30).—Outer side of basis produced beyond base of endopodite as a rounded lobe fringed with long setae. Ischion distinct, there are 2 short spines on its ventral surface. Remainder of endopodite subconical in outline. Its inner side near apex shows indications of division into 3 lobes which bear long setae of differing thicknesses. Inner margin of endopodite bears comb-setae. Two long setae occur on outer margin; there is a pencil of fine setae in angle of lower one. Endite subconical and setose. It terminates in a conical, setose process, below base of which are 3 spines.

Pereion.—Posterior borders of 1st–3rd segments nearly straight with posterior angles bluntly rounded. Epimera of 4th segment slightly produced backwards with posterior angles right-angled. Epimera of 5th–7th segments more markedly produced backwards with angles subacute. Coxal suture lines evident on 3rd–7th segments but inconspicuous. Dorsal surface of pereion smooth. Tergites have covering of pointed scales, which do not appear to be striated, and also bear scale-setae (Fig. 31) each with a narrow pointed scale portion. Large simple setae not present.

Pereiopods.—Large spines on 1st leg each composed of an outer sheath, split at its apex into several fine points, surrounding a coarser central seta. Hyaline scales present on under surface of meros and carpos. Dactylos ends in a simple claw. Dactylar seta bifurcates, and one ramus subdivides dichotomously while the other has branches arising from one main axis. Dactylos of 4th leg shown in Figure 32.

Hyaline scales also occur on under surface of 2nd–4th legs. Outer surface of propodos of 6th and 7th legs has fringe of long scales. Seventh leg shows sexual differentiation; lower region of ischion (Fig. 33) forms a lobe which projects forwards below meros, and under surface of ischion is shallowly indented. In 1st–6th legs, lower part of distal border of ischion slopes back towards basis; its under surface not indented.

Male organ (Fig. 34).—Distal region broadened and rounded; it terminates in a median conical process with folded walls. A slight ridge crosses ventral surface

at base of rounded portion. The two ducts entering organ unite inside it to form one.

Pleon.—Abruptly narrower than pereion. Pleura of 3rd–5th segments small, acute, and adpressed, but visible in dorsal view. Terminal segment trapezoidal,

Figs. 32–41.—*Styloniscus maculosus,* sp. nov.: *32,* dactylos of right 4th leg, anterior view; *33,* meros and ischion of right 7th leg of male, anterior view, *34,* male organ, ventral view; *35,* left 1st pleopod of male, dorsal view; *36,* distal part of endopodite of right 1st pleopod of male, dorsal view; *37,* left 2nd pleopod of male, dorsal view; *38,* exopodite of right 5th pleopod of male, dorsal view; *39,* meros and ischion of right 7th leg of female, anterior view; *40,* right 1st pleopod of female, ventral view; *41,* left 2nd pleopod of female, dorsal view.

with posterior border very slightly curved outwards. Surface of pleon smooth. Tergites bear scales and scale-setae like those on pereion.

First pleopod (Fig. 35).—Protopodite broad; its outer surface rounded and bearing hyaline scales. Exopodite subtriangular, with apex bluntly rounded and

slightly crenate, and outer border not indented. Endopodite subcylindrical, terminating in a long flagelliform process. Distal quarter of process (Fig. 36) densely setose; its apex sharply rounded with 3 sparsely setose pencils projecting from it. Well-developed muscles, supported by a prolongation of 1st sternite of pleon, are inserted at base of endopodite.

Second pleopod (Fig. 37).—Exopodite subquadrangular; it bears setae on inner margin and outer posterior angle. Length of articles of endopodite: 1st 0·27 mm, 2nd 1·24 mm. First article subcylindrical with a broad chitinous thickening on inner surface. Second article tapers to a narrow point and is slightly curved outwards. At base of 2nd article, on inner surface, is a broad chitinous thickening, corrugated on margin. Groups of setae occur below this thickening. There is a narrow, oblique, chitinous thickening on ventral surface of article at about two-fifths of its length behind apex. A groove with strongly chitinized walls extends obliquely down dorsal surface. Apical region of article ornamented with longitudinal ridges of chitin.

Fifth pleopod.—Exopodite (Fig. 38) subtriangular, with comb-setae on lateral borders, a large plumose seta at apex, and a few simple setae on ventral surface near outer border. On dorsal surface, a setose groove for reception of endopodite of 2nd pleopod extends down inner side of exopodite for almost its whole length. Region occupied by groove heavily pigmented.

Uropod.—Posterior border of protopodite level with that of terminal segment. Rami conical. Length of rami: exopodite 0·88 mm, endopodite 0·70 mm.

Female

Length of largest specimen 6·4 mm, breadth 2·6 mm. Female differs from male in the following structures:

Pereiopods.—Hyaline scales not present on under surface of 1st–4th legs. Under surface of ischion of 7th leg (Fig. 39) not indented; lower part of its distal border slopes back towards basis, as in 1st–6th legs of male.

First pleopod (Fig. 40).—Exopodite subtriangular with outer border scarcely indented. Endopodite subtriangular, much smaller than exopodite. No well-developed muscles attached to endopodite.

Second pleopod (Fig. 41).—Endopodite conical; its distal half bears comb-setae. Length of exopodite approximately two-thirds that of endopodite; lengths (along inner border): exopodite 0·42 mm, endopodite 0·61 mm.

Fifth pleopod.—Exopodite not grooved or heavily pigmented.

Habitat

Type locality.—Description is based on specimens found in debris on the ground in a forest of eucalypts and tree ferns at Tarraleah, on 7.x.1957; 19 males and 26 females obtained.

Other localities.—Specimens were found in forest debris near the Lake Highway at Golden Valley, at Notley Gorge, on Mt. Barrow, and in Mt. Field National Park, as well as in a decaying eucalypt log at Collinsvale.

Variations

Background colour of some specimens from Tarraleah is purplish brown instead of true brown. Number of articles in flagellum of 2nd antenna is 5 or 4 in smaller specimens.

STYLONISCUS SQUARROSUS, sp. nov.

Figs. 42–51

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male (Fig. 42)

Size.—Length of largest specimen 5·1 mm, breadth 2·4 mm.

Colour.—Dorsal surface of live animal purplish brown marked with conspicuous unpigmented patches. On pereion there is a large patch at base of each epimeron, and other patches occur between this and mid-line; a pigmented band extends down centre of pereion.

Cephalon.—Vertex has 4 rows of prominent rounded tubercles. Each tubercle bears a large scale-seta. Frontal line absent; supra-antennal line present. Antennary tubercles right-angled. Eyes each composed of 3 ocelli, separated from each other and arranged in a triangle.

First antenna.—Third article spatulate with 9 apical setae.

Second antenna. Length of peduncle 2·10 mm; length of flagellum 0·75 mm. Anterior surface of 5th article of peduncle raised into prominences which form two series, 5 in a dorsal row and 2 in a ventral row. There is a group of large hyaline scale-setae on each prominence. Flagellum has 7 articles.

Left mandible (Fig. 43).—On inner surface of molar process is a slender, sparsely setose pencil of setae.

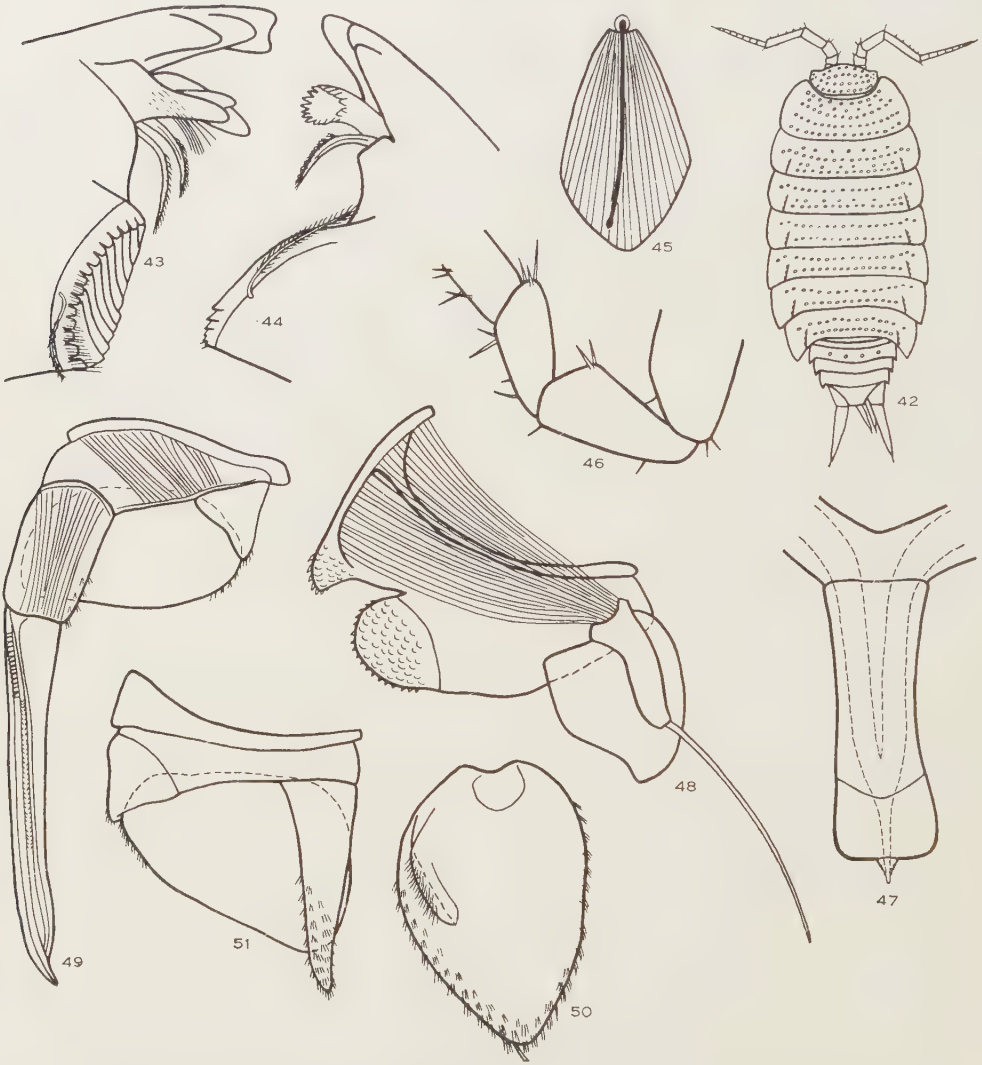
Right mandible (Fig. 44).—On inner side of molar process is a pencil of setae, longer and more densely setose than that on molar process of left mandible. In other respects mandibles as described for *St. maculosus.*

First maxilla, 2nd maxilla, maxilliped.—As described for *St. maculosus.*

Pereion.—Shape of epimera as described for *St. maculosus.* Epimera of 2nd–7th segments each exhibit an oblique tuberculate ridge extending forwards and inwards from posterior margin. Dorsal surface between epimera bears numerous prominent rounded tubercles arranged in transverse rows; 5 rows on 1st segment, 4 rows on 2nd, 3 rows on 3rd, and 2 rows each on 4th–7th segments. On each tubercle is a large hyaline scale-seta (Fig. 45), scale part of which is finely striated, while seta is slightly expanded at the end. Tergites have dense covering of pointed striated scales.

Pereiopods.—First to 6th legs as described for *St. maculosus.* Seventh leg shows no sexual differentiation; lower border of ischion (Fig. 46) straight.

Male organ (Fig. 47).—Distal region rounded and terminating in a small conical process with folded walls. Behind rounded portion, ventral surface crossed by a V-shaped ridge. The two ducts entering organ unite inside it to form one.



Figs. 42-51.—*Styloniscus squarrosus*, sp. nov.: *42*, male specimen, dorsal view; *43*, distal part of left mandible, dorsal view; *44*, distal part of right mandible, dorsal view; *45*, scale-seta on a tubercle on 5th tergite of pereion, dorsal view; *46*, meros and ischion of right 7th leg of male, anterior view, *47*, male organ, ventral view; *48*, left 1st pleopod of male, dorsal view; *49*, right 2nd pleopod of male, dorsal view; *50*, exopodite of right 5th pleopod of male, dorsal view; *51*, left 2nd pleopod of female, dorsal view.

Pleon.—Abruptly narrower than pereion. Pleura of 3rd–5th segments small, acute, and adpressed, but visible in dorsal view. Terminal segment trapezoidal,

with posterior border straight. There is a row of tubercles across 3rd tergite; each tubercle bears a large scale-seta. Remainder of pleon smooth. Tergites covered with pointed striated scales.

First pleopod (Fig. 48).—Exopodite subtriangular with outer border indented. Endopodite subcylindrical, terminating in a long flagelliform process which is simply pointed at apex and lacks setae. Protopodite and muscles as described for *St. maculosus*.

Second pleopod (Fig. 49).—Exopodite as for *St. maculosus*. Length of articles of endopodite: 1st 0·30 mm, 2nd 0·85 mm. First article subcylindrical with comb-setae on outer surface. Second article tapers evenly to a bluntly pointed apex, slightly bent outwards at the tip. On dorsal surface a groove with strongly chitinized walls extends obliquely down length of article. At base of article, inner wall of groove is ornamented with blunt tooth-like processes. In middle third, walls of groove exhibit small, backwardly sloping, chitinous ridges.

Fifth pleopod.—Exopodite (Fig. 50) subtriangular, with setae as described for *St. maculosus*, and, in addition, with comb-setae on dorsal surface of apical region. Groove for endopodite of 2nd pleopod occupies approximately half length of exopodite. Region occupied by groove not heavily pigmented.

Uropod.—Length of rami: exopodite 1·00 mm, endopodite 0·70 mm. Otherwise as described for *St. maculosus*.

Female

Length of largest specimen 6·2 mm, breadth 3·1 mm. Female differs from male in the following structures:

Pereiopods.—Hyaline scales not present on under surface of meros and carpos of 1st–4th legs.

First pleopod.—As described for *St. maculosus*.

Second pleopod (Fig. 51).—Endopodite conical; its distal half bears comb-setae. Length of exopodite approximately four-fifths that of endopodite; lengths (along inner border): exopodite 0·35 mm, endopodite 0·44 mm.

Fifth pleopod.—Exopodite not grooved.

Habitat

Type locality.—Description is based on specimens found in debris and under wood on the ground at altitudes of 1500–3000 ft on Mt. Wellington; collections made were as follows: 15.v.1956, 2 males, 8 females; 22.x.1956, 6 males, 5 females; 6.iii.1957, 1 male; 28.v.1957, 4 males, 3 females.

Other localities.—Specimens were found in a decaying eucalypt log at Collinsvale, and in debris in the Arve Forest.

Variations

Background colour of some specimens is a light reddish brown. Some smaller specimens are dark brown, with unpigmented patches less conspicuous than in larger specimens. Number of articles in flagellum of 2nd antenna is 6, 5, or 4 in smaller specimens.

Genus NOTONISCUS Chilton, nom. emend.

Notoniscus Chilton, 1915*a*, p. 418.
Chiltonia Arcangeli, 1923, p. 314 (non Stebbing, 1899).
Chiltonella Vandel, 1945, p. 236, nomen nudum.
Chiltonella Vandel, 1952, p. 96.
?*Paranotoniscus* Barnard, 1932, p. 202.

Type species *Haplophthalmus helmsii* Chilton, 1901.

Chilton established *Notoniscus* for two species, *N. helmsii* (Chilton 1901) from New Zealand and *N. australis* (Chilton 1909) from Campbell I., N.Z., originally placed in *Haplophthalmus* Schöbl, 1860. He noted that *Notoniscus* differed from *Haplophthalmus* in the character of the eyes, and in the fact that the first 3 instead of the first 2 segments of the pleon had the pleura very small or absent.

Chilton (1915*a*, p. 424) erected a new species, *Haplophthalmus tasmanicus*, from Tasmania. This differed from *Notoniscus* and agreed with *Haplophthalmus* in having large pleural expansions on the 3rd segment of the pleon. However, Chilton stated that it differed from the description of *Haplophthalmus* given by Sars (1899) in having the eyes not simple but composed of 3 ocelli and the segments of the pereion not discontiguous laterally. Arcangeli (1923, p. 314) considered these characters sufficient to separate *H. tasmanicus* from *Haplophthalmus*, and he designated it as the type of a new genus, *Chiltonia*.

Barnard (1932, p. 202) erected a new genus, *Paranotoniscus*, distinguished from *Notoniscus* by the presence of better-developed pleura on the 3rd segment of the pleon. Barnard's diagnosis of *Paranotoniscus* did not distinguish it from *Chiltonia* Arcangeli; however, he made no reference to this genus.

Jackson (1941, p. 8) nominated *H. helmsii* as the type species of *Notoniscus*.

Vandel (1945, p. 236) noted the occurrence in Tasmania of "*Chiltonella tasmanica* (Chilton)", and later (1952, p. 94) listed a genus as "*Chiltonella* Arcangeli". On p. 96 of this (1952) paper he stated (the following is a translation from the original French):

> "Arcangeli (1923, p. 314) has established the genus *Chiltonella* in order to place there *Haplophthalmus tasmanicus* Chilton, 1915, a species of which only a single example has been known until now. *Chiltonella* differs from *Notoniscus* in the presence of well-developed neopleurons on the third pleonite."

But the reference to Arcangeli (1923) listed by Vandel (p. 110) in his bibliography is that in which Arcangeli named his genus *Chiltonia*.

The name *Chiltonia* was preoccupied in 1923, having been used for a genus of amphipods by Stebbing (1899, pp. 397, 408). However, Vandel gave no indication that the replacement of Arcangeli's name was due to knowledge of its preoccupation. *Chiltonella* was not mentioned in the list of generic names given by Neave (1939–40, 1950) or in the Zoological Records covering literature for the years 1923–1956. The earliest published reference to *Chiltonella* appears to be that given by Vandel in 1945, and as it is not accompanied by any diagnosis or description, this reference should be regarded as a nomen nudum. In 1952, Vandel

characterized *Chiltonella* by referring to it *H. tasmanicus* and by noting its distinction from *Notoniscus*. *Chiltonia* Arcangeli and *Chiltonella* Vandel are absolute synonyms, as both have been used for the one genus which contains *H. tasmanicus* as the type and only species. As *Chiltonia* is unavailable, I propose to refer to this genus as *Chiltonella*, regardless of confusion in the earlier use of the second name.

Vandel (1952, p. 96) noted that, although the sexual characters of *Ch. tasmanica* were not known, *Chiltonella* probably belonged in his subfamily Notoniscinae. I have collected specimens which agree with Chilton's description of *H. tasmanicus*, and whose characters also conform with Vandel's (1952, pp. 94, 96) diagnoses of family Styloniscidae and subfamily Notoniscinae. His inclusion of *Chiltonella* in these divisions is therefore confirmed.

In addition, I have collected in Tasmania specimens which I assign to *N. australis*, after a comparison of their characters with Chilton's (1915*a*, p. 421) description of this species. On comparing the Tasmanian examples of *N. australis* and *Ch. tasmanica*, I have found, apart from the differing development of the 3rd pleura, only two major differences between them, namely (1) the arrangement of tubercles on cephalon and pereion, and (2) certain characters of those pleopods which show sexual differentiation. A comparison of specimens of *Ch. tasmanica* with Chilton's (1915*a*, p. 418) description of *N. helmsii* indicates that *Ch. tasmanica* differs from this, the type species of *Notoniscus*, in the same respects. I consider these differences in tuberculation and sexual characters of pleopods to be only of specific value. Such differences have been regarded as specific within the allied genus *Styloniscus*; also *N. helmsii* and *N. australis* are distinguished by a different arrangement of tubercles.

In comparing characters of *H. tasmanicus* with generic characters of *Haplophthalmus*, Chilton claimed that the segments of the pereion in this species are not discontiguous laterally, but in his actual description of the species he described them as being nearly contiguous. In my specimens of *Ch. tasmanica* the epimera are slightly discontiguous; therefore the species does not differ from *Notoniscus* in this regard.

There remains only the difference in the development of the 3rd pleura to distinguish *Chiltonella* from *Notoniscus* on a generic level. As their species are basically similar in other respects, I do not consider that a separation of the monotypic genus *Chiltonella*, due to this one distinctive character, is warranted. I therefore propose to extend the limits of *Notoniscus* to include species in which the pleura of the 3rd segment of the pleon are well developed, and to transfer *Ch. tasmanica* to this genus. As *Ch. tasmanica* is the type and only species of *Chiltonella*, this name becomes a synonym of *Notoniscus*. Although Chilton used the character of the pleon in distinguishing *Notoniscus* from *Haplophthalmus*, with the limits of the former so extended these two genera still remain clearly distinct, as they now belong in different families, the Styloniscidae and Trichoniscidae respectively, and are therefore distinguished by the characters which separate these families.

In his diagnosis of *Notoniscus*. Chilton described the eyes as having more than one visual element, but did not limit the number. Eyes composed of 3 ocelli are exhibited by all three species now included in *Notoniscus*. Chilton stated antennules, antennae, mouthparts, and dactylar seta of pereiopods to be as in *Trichoniscus*. It seems likely that he was comparing these structures in *Notoniscus* with those of New Zealand species which he placed in *Trichoniscus*, and which were transferred by Vandel (1952) to *Styloniscus*. In the species of *Notoniscus* and *Styloniscus* found in Tasmania these structures are very alike. Therefore, as *Trichoniscus* and *Notoniscus* have now been placed in different families, in diagnosing *Notoniscus* I propose to note its similarities with *Styloniscus* rather than with *Trichoniscus*. As well as the structures listed by Chilton, the male organ and male and female pleopods in *Notoniscus* are of a similar kind to those found in *Styloniscus*. I therefore propose the following diagnosis of *Notoniscus*, which is emended from that given by Chilton (1915*a*, p. 418) in the points just discussed.

Generic Diagnosis

Body oblong, central portion moderately convex, dorsal surface sculptured and bearing ridges or tubercles. Cephalon with the front triangularly produced, antennary tubercles directed downwards, rather small, with extremity subacute. Epimera lamellarly expanded, projecting almost horizontally, discontiguous. Pleon not abruptly contracted; pleura of 3rd segment either small or well developed, those of 4th and 5th segments well developed, lamellar; terminal segment trapezoidal with truncate posterior margin. Eyes each composed of 3 ocelli. Antennules, antennae, and mouthparts as in *Styloniscus* Dana, 1852. Legs rather short, not increasing much in length posteriorly; dactylar seta as in *Styloniscus*. Male organ, and pleopods of both sexes, of the same kind as in *Styloniscus*. Uropoda with rami rather widely separated, subequal.

Remarks

The diagnosis of *Paranotoniscus* given by Barnard (1932, p. 202) does not differentiate this genus from *Notoniscus* as defined here. His figures (6,*a*,*e*) of his species *P. capensis* and *P. montanus* show that the pleura of the 3rd segment of the pleon in these species are expanded, but are narrower and more acute than those of the 4th and 5th segments, and so are intermediate between those of *N. helmsii* and *N. australis* on one hand and those of *N. tasmanicus* on the other. Thus it appears likely that *Paranotoniscus* might also be regarded as a synonym of *Notoniscus*. However, as Barnard's descriptions of four of his five species are brief, I should hesitate to consider this synonymy as definite without a comparison of specimens from the two genera.

KEY TO SPECIES OF THE GENUS NOTONISCUS REPRESENTED IN TASMANIA

Tubercules on pereion forming 4 rows in male, 5 rows in female; 3rd pleura small compared with 4th and 5th pleura ..... *australis*

Tubercles on pereion forming 6 rows in both sexes; 3rd pleura as large as 4th and 5th pleura ..... *tasmanicus*

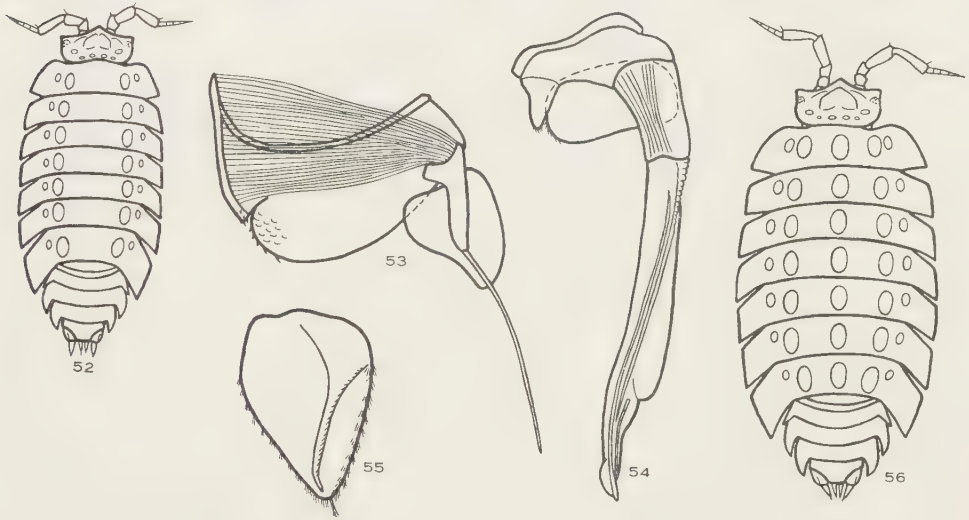
Notoniscus australis (Chilton)

Figs. 52–56

Haplophthalmus australis Chilton, 1909, p. 662, fig. 17.
Notoniscus australis Chilton, 1915*a*, p. 421, figs. 9–22.

Location of type specimen.—Canterbury Museum, Christchurch, N.Z.

The descriptions of examples of this species from Campbell I., N.Z., given by Chilton (1909, 1915*a*) were based on female specimens. As Chilton (1915*a*, p. 423) himself pointed out, the appendage which he (1909, p. 664, fig. 17*e*) described and figured as the 2nd pleopod of a male was actually that of a female; Chilton then stated that he had not found a male specimen. A description of both male and female specimens of Tasmanian material assigned to *N. australis* is therefore given.



Figs. 52–56.—*Notoniscus australis* (Chilton): *52*, male specimen, dorsal view; *53*, left 1st pleopod of male, dorsal view; *54*, left 2nd pleopod of male, dorsal view; *55*, exopodite of left 5th pleopod of male, dorsal view; *56*, female specimen, dorsal view.

Male (Fig. 52)

Size.—Length of largest specimen 3·0 mm, breadth 1·5 mm.

Colour.—Dorsal surface of live specimen dark brown.

Cephalon.—Centre of vertex occupied by a large pyramidal tubercle; small tubercles occur on remainder of vertex. Anterior region of cephalon produced forwards as an acute triangular process. Antennary tubercles acute-angled. Eyes each composed of 3 ocelli set on a rounded prominence; ocelli of each eye separated from each other and arranged in a triangle.

First antenna.—Apex of 3rd article oblique, with one side sharply pointed; it bears 3 long setae.

Second antenna.—Length of peduncle 0·71 mm; length of flagellum 0·22 mm. All articles of antenna covered with scales, but no prominent groups of hyaline scales on 4th and 5th articles of peduncle. Flagellum has 4 articles.

Mandibles, 1st and 2nd maxillae.—As described for *N. tasmanicus*.

Maxilliped.—Epipodite widest at base and tapering to a subacute apex. Endopodite and endite as described for *N. tasmanicus*.

Pereion.—Shape of epimera as described for *N. tasmanicus*. Each segment bears 4 rounded tubercles which together form 4 longitudinal rows down pereion. The 2 inner rows made up of large tubercles; those forming the 2 outer rows smaller and less conspicuous. No row of prominent tubercles down mid-line of pereion. Dorsal surface bears scattered scale-setae and covering of rounded scales. Lateral margins of segments bordered with triangular scales.

Pereiopods.—Large hyaline scales not present on under surface of 1st and 2nd legs. Otherwise legs as described for *N. tasmanicus*.

Male organ.—As described for *N. tasmanicus*.

Pleon.—Not abruptly narrower than pereion and not tuberculate. Pleura developed on 3rd segment, but they are narrow and acute, not extending outwards as far as general outline of body. Pleura of 4th and 5th segments large, semi-crescentic, and sharply directed backwards; they form part of general outline of body. Terminal segment trapezoidal with posterior border straight. Tergites bear scales and scale-setae like those on pereion.

First pleopod (Fig. 53).—Exopodite subtriangular with outer border indented; apex not crenate. Endopodite subcylindrical, terminating in a long flagelliform process which is simply pointed at apex and lacks setae. Protopodite and muscles as described for *N. tasmanicus*.

Second pleopod (Fig. 54).—Exopodite as described for *N. tasmanicus*. Length of articles of endopodite: 1st 0·16 mm, 2nd 0·58 mm. First article subcylindrical. Inner side of 2nd article curves inwards abruptly at about two-sevenths of its length from apex, so that apex is asymmetrical, continuous with outer side of endopodite; apical region tapers to a sharp point. Just behind this point is a rounded chitinous prominence on outer side. A groove with strongly chitinized walls extends obliquely down dorsal surface of article. Near its base, inner wall of groove bears blunt tooth-like processes.

Fifth pleopod.—Exopodite (Fig. 55) subtriangular, with comb-setae on lateral borders, and plumose and simple setae as described for *N. tasmanicus*. Groove for endopodite of 2nd pleopod extends down whole length of exopodite. Area occupied by groove heavily pigmented.

Uropod.—Outer region of protopodite, marked off on dorsal surface by a ridge in line with outer edge of exopodite, forms only a narrow flattened expansion. Length of rami: exopodite 0·15 mm, endopodite 0·19 mm. Otherwise as described for *N. tasmanicus*.

Female (Fig. 56)

Length of largest specimen: 4·6 mm, breadth 2·3 mm. Female differs from male in the following structures:

Tubercles on pereion.—Dorsal surface of each segment bears 5 rounded tubercles which together form 5 longitudinal rows down pereion. Tubercles forming outermost row on each side more conspicuous than in male.

First pleopod.—As described for *N. tasmanicus.*

Second pleopod.—Endopodite conical; its distal region bears comb-setae. Length of exopodite approximately one-third that of endopodite; lengths (along inner border): exopodite 0·13 mm, endopodite 0·38 mm.

Fifth pleopod.—As described for *N. tasmanicus.*

Habitat

Description is based on specimens found in debris on the ground in a myrtle forest at Collinsvale; collections made were as follows: 12.vi.1957 and 19.vi.1957, 60 males, 114 females; 13.xi.1957, 60 males, 84 females. One female specimen was found in forest debris at Tarraleah, and one in debris in the Arve Forest.

Variation

In small female specimens, approximately less than 2·3 mm long, median row of tubercles on pereion is less conspicuous than inner lateral rows. Tuberculation of these young females thus approaches condition found in males.

Remarks

Chilton (1915*a*, p. 423) described and figured the maxilliped as having the epipodite rounded at its extremity and slightly narrower near its base, and the endopodite formed of a single article. In the Tasmanian specimens the epipodite of the maxilliped is widest at its base and its apex is subacute; also the ischion is distinct from the remainder of the endopodite.

Chilton (1909, p. 662), with regard to specimens from Campbell I., stated "The animal runs with great rapidity". However, the speed of walking of the specimens of *N. australis* from Collinsvale is rather slow when compared for example with that of specimens of *Styloniscus thomsoni* which were found in the same samples of debris.

Notoniscus tasmanicus (Chilton)

Figs. 57–72

Haplophthalmus tasmanicus Chilton, 1915*a*, p. 424, fig. 23.
Chiltonia tasmanica Arcangeli, 1923, p. 314, pl. 7, fig. 6.
Chiltonella tasmanica Vandel, 1945, p. 236, nomen nudum.
Chiltonella tasmanica Vandel, 1952, p. 96.

Location of type specimen.—Canterbury Museum, Christchurch, N.Z.

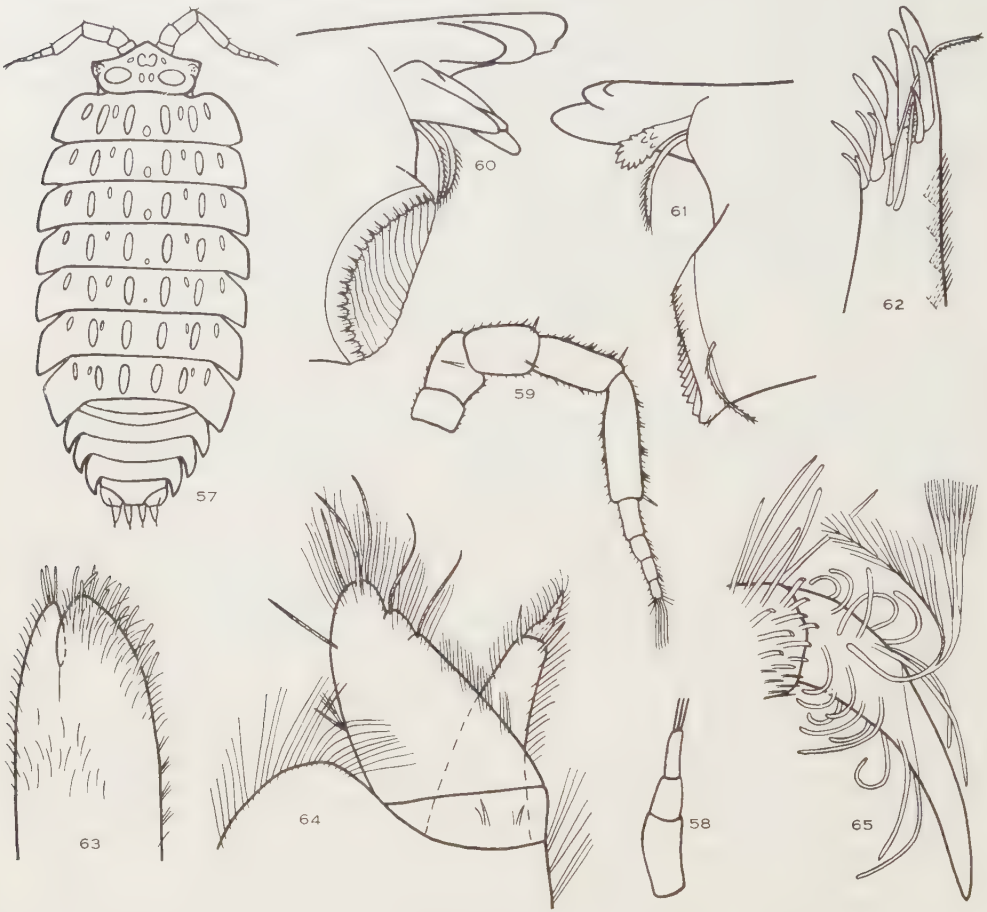
As Chilton had only one example of this species he described only characters which could be observed without dissecting the animal. A detailed description of my specimens is therefore given.

Male (Fig. 57)

Size.—Length of largest specimen 4·50 mm, breadth 2·25 mm.

Colour.—Dorsal surface of live specimen dark brown.

Cephalon. Near posterior margin of vertex are 2 large rounded tubercles with a pair of smaller tubercles between them. In front of these is a large, median, bituberculate prominence with a small tubercle on each side of it. Anterior region of cephalon produced forwards as an acute triangular process. Antennary tubercles



Figs. 57–65.—*Notoniscus tasmanicus* (Chilton):—*57,* male specimen, dorsal view; *58,* left 1st antenna, ventral view; *59,* left 2nd antenna, ventral view; *60,* distal part of left mandible, dorsal view; *61,* distal part of right mandible, dorsal view; *62,* distal part of outer lobe of left 1st maxilla, ventral view; *63,* distal part of right 2nd maxilla, ventral view; *64,* distal part of right maxilliped, ventral view; *65,* dactylos of left 7th leg, anterior view.

right-angled. Eyes each composed of 3 ocelli set on a rounded prominence; ocelli of each eye separated from each other and arranged in a triangle.

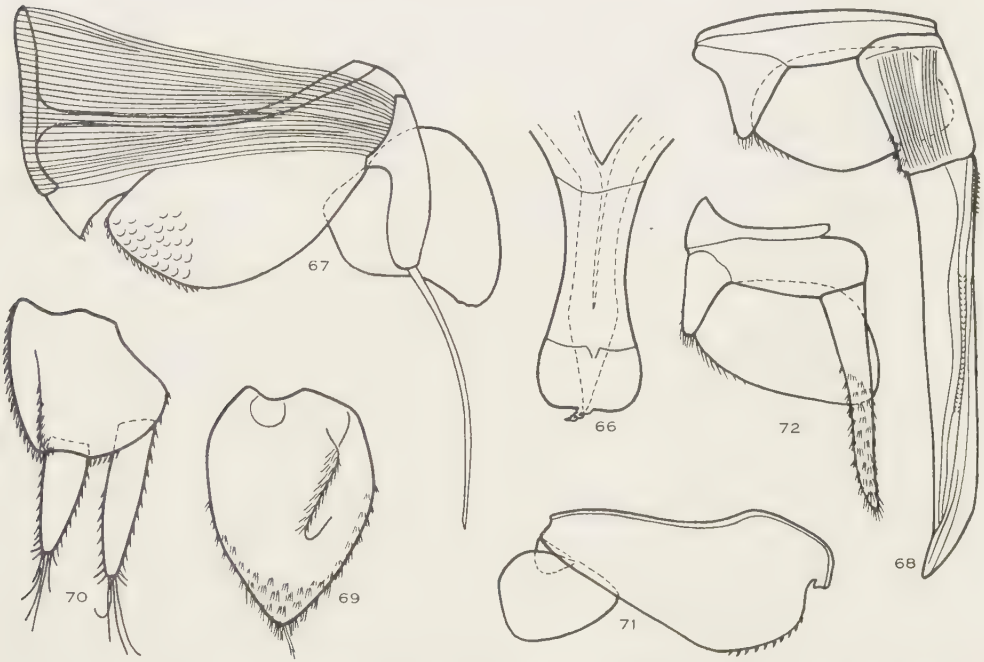
First antenna (Fig. 58).—Third article narrow; it has 3 long apical setae.

Second antenna (Fig. 59).—Length of peduncle 1·43 mm; length of flagellum 0·37 mm. All articles have covering of scales. Groups of larger hyaline scales present on 4th and 5th articles of peduncle, but these are not raised on tubercles. Flagellum has 4 articles.

Left mandible (Fig. 60).—Incisor process consists of a bifid tooth and 2 simple teeth. Lacinia mobilis ends in 3 teeth; behind its base are 2 pencils of setae. Molar process triturating; no molar pencil.

Right mandible (Fig. 61).—Incisor process formed of 3 simple teeth. Lacinia mobilis club-shaped with a ring of tooth-like processes at apex; 1 pencil of setae behind its base. Molar process bears a slender pencil of setae.

First maxilla.—Outer lobe (Fig. 62) ends in 11 simple teeth and 2 slender processes. Latter are set at an angle to long axis of lobe; their distal ends bear short setae. Inner lobe bears 3 setose processes.



Figs. 66–72.—*Notoniscus tasmanicus* (Chilton):—*66*, male organ, ventral view; *67*, left 1st pleopod of male, dorsal view; *68*, left 2nd pleopod of male, dorsal view; *69*, exopodite of left 5th pleopod of male, dorsal view; *70*, left uropod, dorsal view; *71*, left 1st pleopod of female, ventral view; *72*, left 2nd pleopod of female, dorsal view.

Second maxilla (Fig. 63).—Apical region divided into 2 rounded lobes. Outer lobe bears 3 spines and a fringe of fine setae. Inner lobe bears coarse and fine setae.

Maxilliped (Fig. 64).—Epipodite tapers to an acute apex. Outer side of basis projects beyond base of endopodite as a rounded lobe fringed with very long setae. Ischion distinct; 2 short spines on its ventral surface. Remainder of endopodite subconical with its inner border showing indications of division into 3 lobes which bear setae of differing thicknesses. Inner border below lobes bears comb-setae. On outer border are 2 large setae, with a pencil of fine setae near

lower one. Endite subconical and setose. It terminates in a conical setose process, below base of which are 3 spines.

Pereion.—Dorsal surface between epimera strongly convex. Epimera large, subrectangular, and slightly discontiguous laterally. Epimera of 1st segment nearly transverse, those of 2nd segment slightly directed backwards, those of 3rd–7th segments slope increasingly further backwards. Each segment bears 6 prominent oval tubercles, which together form 6 longitudinal rows down pereion. The 4 inner rows made up of large tubercles which occupy greater part of length of segments. Tubercles forming outermost row on each side slightly oblique and smaller than those forming inner rows. Small tubercles present between those of main rows. Dorsal surface bears scattered scale-setae and covering of rounded scales. Lateral borders of segments have dense fringe of long pointed scales.

Pereiopods.—Large spines on 1st leg each have apex of outer sheath divided into several fine points, surrounding a coarser central seta. Large hyaline scales present on under surface of meros and carpos. Dactylos ends in a simple claw. Dactylar seta bifurcates, and one ramus subdivides dichotomously while the other has branches arising from one main axis. Dactylos of 7th leg shown in Figure 65.

A few hyaline scales occur on under surface of meros and carpos of 2nd leg. Outer surface of propodos of 6th and 7th legs has fringe of long scales. Seventh leg shows no sexual differentiation.

Male organ (Fig. 66).—Apical region broadened and rounded; it terminates in a small conical process with folded walls. On ventral surface, apical region is crossed by a ridge. The two ducts entering organ unite inside it to form one.

Pleon.—Not abruptly narrower than pereion and not tuberculate. Pleura of 3rd–5th segments large, semicrescentic, and sharply directed backwards; all 3 form part of outline of body. Terminal segment trapezoidal with posterior border straight. Tergites bear scales and scale-setae like those on pereion.

First pleopod (Fig. 67).—Protopodite broad; its outer side bears hyaline scales. Exopodite subtriangular with outer border indented; its apex slightly crenate. Endopodite subcylindrical, terminating in a long flagelliform process which is simply pointed at apex and lacks setae. Well-developed muscles, supported by a prolongation of 1st sternite of pleon, are inserted at base of endopodite.

Second pleopod (Fig. 68).—Exopodite subrectangular with setae on outer posterior angle. Length of articles of endopodite: 1st 0·25 mm, 2nd 0·75 mm. First article subcylindrical with comb-setae on inner surface. Second article tapers evenly to a bluntly pointed apex, slightly bent outwards. On dorsal surface, a groove with strongly chitinized walls extends obliquely down its whole length. Near base of article, inner wall of groove bears tooth-like processes. In middle third, both walls of groove bear small, backwardly sloping, chitinous ridges.

Fifth pleopod.—Exopodite (Fig. 69) subtriangular. Comb-setae present on both lateral borders and across dorsal surface of apical region. There are a plumose seta at apex and a few simple setae on ventral surface near apex. On dorsal surface a groove for reception of endopodite of 2nd pleopod occupies approximately half length of exopodite.

Uropod (Fig. 70).—Protopodite subtriangular; its posterior border level with that of terminal segment. Exopodite terminal in position on protopodite. Outer region of protopodite forms a flattened expansion, delimited on dorsal surface by a ridge in line with outer edge of exopodite. Endopodite inserted on ventral surface of protopodite near its posterior border. Rami conical. Length of rami: exopodite 0·23 mm, endopodite 0·32 mm.

Female

Length of largest specimen 4·7 mm, breadth 2·4 mm. Female differs from male in the following structures:

Pereiopods.—Hyaline scales not present on under surface of meros and carpos of 1st and 2nd legs.

First pleopod (Fig. 71).—Exopodite subtriangular with outer border not indented. Endopodite rounded, much smaller than exopodite. Well-developed muscles not present.

Second pleopod (Fig. 72).—Endopodite conical; its distal region bears comb-setae. Length of exopodite approximately half that of endopodite; lengths (along inner border): exopodite 0·27 mm, endopodite 0·55 mm.

Fifth pleopod.—Exopodite not grooved.

Habitat

Description is based on specimens found in debris on the ground in a myrtle forest at Collinsvale, on 12.vi.1957 and 19.vi.1957; 16 males and 26 females obtained. Three female specimens were collected by Professor Hickman on 1.xii.1955, from moss in the Arve Forest.

The specimen described by Chilton (1915*a*) was found "under rotten logs, Fern Tree Gully, Hobart, Tasmania".

Variation

Bodies of some specimens exhibit unpigmented areas which are particularly frequent on and near 5th segment of pereion.

Remarks

Chilton (1909, pp. 661–2) mentioned an undescribed species of *Haplophthalmus* from Tasmania; presumably this was *H. tasmanicus*. The synonymy of the species, and its position in *Notoniscus*, is discussed in the section on the genus.

VII. Family **SCYPHACIDAE**

Key to Genera of Scyphacidae Represented in Tasmania

Animal not able to enrol; dorsal surface of body shallowly convex ..... *Deto*
Animal able to enrol; dorsal surface of body strongly convex ..... *Actaecia*

Genus DETO Guérin

Deto Guérin, 1836, text to pl. 14.

Type species *Deto echinata* Guérin, 1836.

Generic Diagnosis

The following generic diagnosis is taken from Chilton (1915*b*, p. 438):

"General shape of body oblong-oval, somewhat depressed; animal not capable of rolling itself into a ball; epimera lamellarly expanded; dorsal surface usually with spines or tubercles which are better developed in the male than in the female; pleon not abruptly narrower than peracon; epimera of third, fourth and fifth segments well developed. Head with lateral processes forming broad lobes.

Eyes of moderate size, with many ocelli.

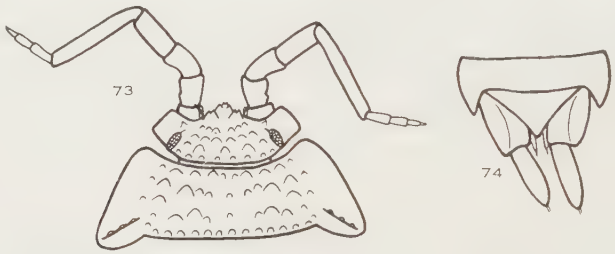
Antennae with flagellum four-jointed.

Mandibles with one pencil behind the cutting-edge.

Maxillipedes with palp longer than masticatory lobe, and showing indications of being formed of three or four joints.

Exopoda of the pleopoda opercular, and containing no special branchial organ.

Uropoda produced, reaching considerably beyond the terminal segment."



Figs. 73 and 74.—*Deto marina* (Chilton):—*73*, cephalon, 2nd antennae and 1st segment of pereion, dorsal view; *74*, fifth and terminal segments of pleon and uropods of male, dorsal view.

Deto marina (Chilton)

Figs. 73, 74

Philougria marina Chilton, 1884, p. 464, pl. 11.
Philygria marina Chilton, 1886, p. 161, pl. 5, fig. 7.
Deto marina Budde-Lund, 1906, p. 85, pl. 4, figs. 39–41.

Location of type specimens.—Canterbury Museum, Christchurch, N.Z.

Distinguishing Characters

Length of largest male specimen 11·0 mm, breadth 5·5 mm; length of largest female specimen 10·0 mm, breadth 5·0 mm.

Live specimen greenish yellow, spotted with black chromatophores. Animal not able to enrol.

Vertex of cephalon (Fig. 73) covered with scale-bearing tubercles. Antennary lobes square in outline, standing out obliquely from cephalon. Eyes compound. Flagellum of 2nd antenna has 4 articles.

Posterior borders of all epimera slope backwards; their posterior angles sharply rounded. An oblique tuberculate ridge extends inwards and forwards from above posterior angle of each epimeron. Dorsal surface of pereion exhibits large scale-bearing tubercles, but no long spines.

Pleon not abruptly narrower than pereion. Pleura of 3rd–5th segments large and subacute. Terminal segment (Fig. 74) triangular with sides slightly indented and apex acute. Dorsal surface of pleon granulate. Exopodites of pleopods have no conspicuous blood vessels and no pseudotracheae. Protopodite of uropod (Fig. 74) quadrangular, flattened on outer side, with a longitudinal ridge down dorsal surface. The two protopodites do not meet in mid-line. Exopodite lanceolate, terminal in position on protopodite. Endopodite conical and inserted anteriorly on ventral surface of protopodite, near its inner margin. In female, exopodite of uropod is shorter in relation to protopodite and endopodite than in male. Lengths in a male specimen: protopodite 1·20 mm, exopodite 1·20 mm, endopodite 0·60 mm; lengths in a female specimen: protopodite 0·90 mm, exopodite 0·68 mm, endopodite 0·45 mm.

Habitat

Description is based on specimens found under stones near high-tide level on a rocky shore at Roaring Beach, South Arm; collections made were as follows: 28.ii.1957, 7 males, 11 females; 8.iii.1957, 12 males, 16 females; 22.iii.1957, 14 males, 9 females. Other specimens were found under similar conditions at Tinderbox, Hawley, and Low Head, East Tamar.

Genus ACTAECIA Dana

Actaecia Dana, 1853, pp. 735–6.
Cylloma Budde-Lund, 1879, p. 8, nomen nudum.
Cylloma Budde-Lund, 1885, p. 46.

Type species *Actaecia euchroa* Dana, 1853.

Generic Diagnosis

The following generic diagnosis is taken from Chilton (1901, p. 130):

"Body convex, capable of rolling into a ball, surface spiny. Metasome not abruptly contracted, terminal segment very short. Flagellum of antennae 4-jointed. Eyes very large and prominent, on oval elevations along the sides of the head. Maxillipedes with the terminal portion large, lamellar. Legs rather short, not increasing much in length posteriorly. None of the opercular plates of the pleopoda with air-cavities. Uropoda short, not projecting much beyond the outline of the body; base broad and flattened, outer portion produced, outer ramus short, inserted at the end of the base near the inner margin; inner ramus slender."

Key to Species of the Genus Actaecia Represented in Tasmania

Fourth and 5th pleura with posterolateral borders rounded; protopodite of uropod longer than broad, with region to outer side of exopodite forming a rounded lobe ..... *euchroa*

Fourth and 5th pleura with posterolateral borders straight; protopodite of uropod slightly broader than long, with region to outer side of exopodite straight posteriorly .. *pallida*

Actaecia euchroa Dana

Figs. 75–90

Actaecia euchroa Dana, 1853, p. 735, pl. 48, fig. 6.

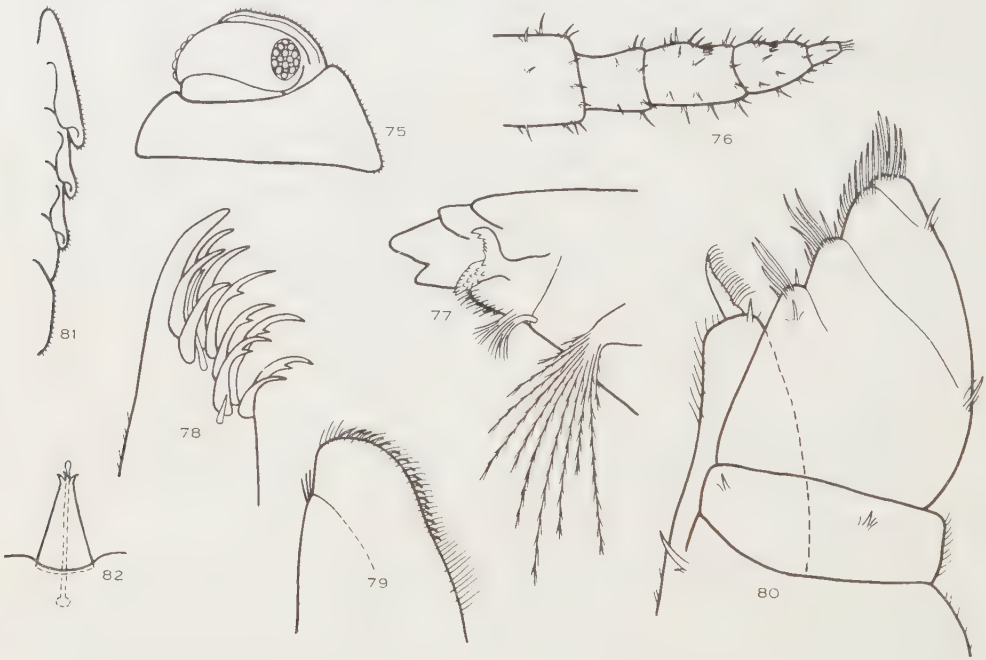
A description given by Thomson (1893, p. 56) of examples of *A. euchroa* from Eaglehawk Neck is incomplete and contains some minor errors. My

Tasmanian specimens differ in an important character from New Zealand examples described by Chilton (1901, p. 130). The following account of further material from Eaglehawk Neck is therefore given.

Male

Size.—Length of largest specimen 5·6 mm, breadth 2·7 mm.

Colour.—Dorsal surface of live animal white, marked with groups of black and orange-brown chromatophores.



Figs. 75–82.—*Actaecia euchroa* Dana: *75,* cephalon, dorsolateral view, showing right eye; *76,* flagellum of right 2nd antenna, dorsal view; *77,* distal part of right mandible, dorsal view; *78,* distal part of outer lobe of right 1st maxilla, ventral view; *79,* distal part of right 2nd maxilla, ventral view; *80,* distal part of left maxilliped, ventral view; *81,* left epimera of 1st–5th segments of pereion, ventral view, showing ridges on 1st–3rd epimera; *82,* spine on lateral border of 1st segment of pereion, dorsal view.

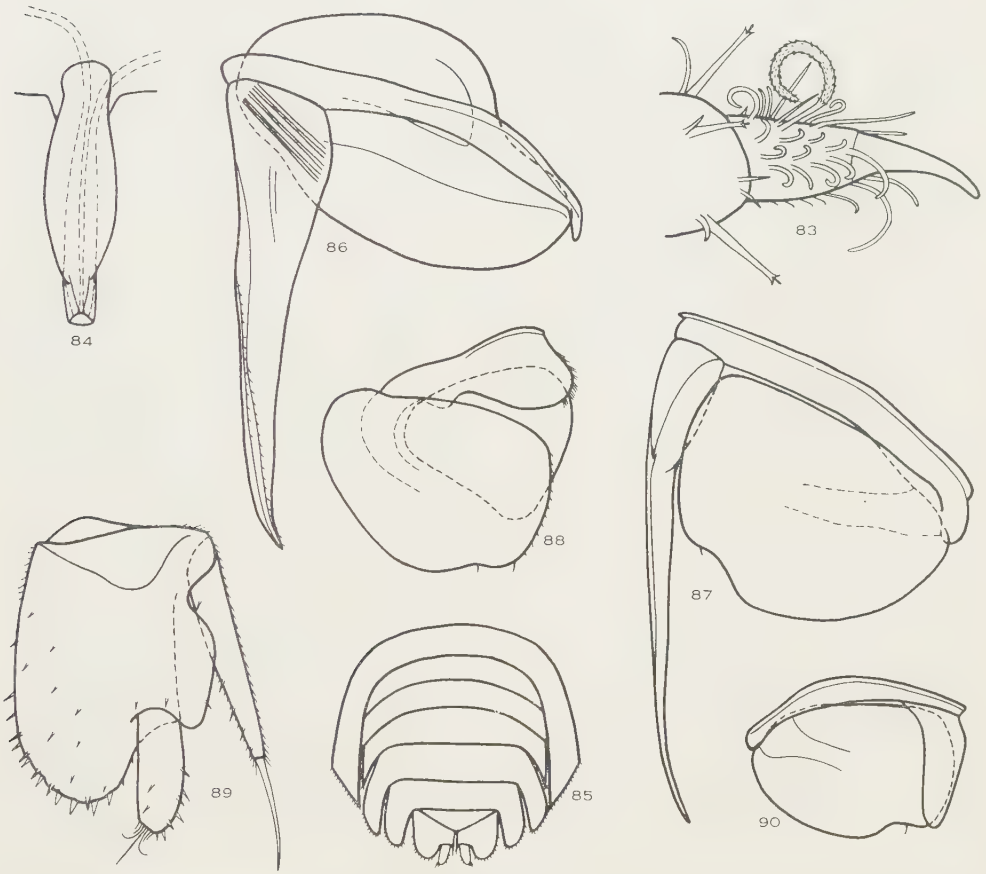
Cephalon.—Maxillipedal somite distinct. Frontal line forms a sharp curved ridge, slightly flattened in centre, and bordered with spines. A supra-antennal line not clearly defined. Antennary tubercles not developed. Eyes (Fig. 75) oval, each composed of 14 ocelli.

First antenna.—Triarticulate; 3rd article has 3 apical setae.

Second antenna.—Length of peduncle 2·51 mm; length of flagellum 0·55 mm. Peduncle and flagellum set with spines, each consisting of an outer sheath, split near the end into several short points, surrounding a central seta, clubbed at its apex; there is a large scale against base of spine. Flagellum (Fig. 76) has 4 articles.

Second and 3rd articles each have an indentation in outer surface in which is set a group of simple spines. Length of 4th article less than twice its greatest breadth; length (excluding apical setae) 0·065 mm; breadth 0·036 mm.

Left mandible.—Incisor process consists of 1 bifid tooth and 2 simple teeth. Lacinia mobilis ends in 3 teeth. Setose lobe bears 2 pencils of setae; 1 pencil behind lobe. Molar portion represented by a subcylindrical process bearing a tuft of plumose setae.



Figs. 83–90.—*Actaecia euchroa* Dana: *83*, dactylos of left 2nd leg, anterior view; *84*, male organ, ventral view; *85*, seventh segment of pereion, pleon, and uropods, dorsal view; *86*, right 1st pleopod of male, dorsal view; *87*, left 2nd pleopod of male, ventral view; *88*, right 3rd pleopod of male, ventral view; *89*, left uropod, dorsal view; *90*, left 2nd pleopod of female, dorsal view.

Right mandible (Fig. 77).—Incisor process consists of 4 simple teeth. Lacinia mobilis divides into 2 processes which bear small, tooth-like projections. Setose lobe bears 1 pencil of setae; 1 pencil behind lobe. Molar portion like that of left mandible.

First maxilla.—Outer lobe (Fig. 78) ends in 11 teeth, of which outer 5 and 2nd innermost one are simple and other 5 are bifid. There is a long slender process set among outer teeth, and a short spine on ventral surface. Outer corner of inner lobe ends in a sharp spine; inner lobe bears 2 setose processes.

Second maxilla (Fig. 79).—Division into 2 lobes indicated by an oblique suture line beginning at an indentation in outer margin of maxilla. Apex of outer lobe bears a few spines. Inner lobe bears coarse and fine setae on margins, and fine setae extend over its dorsal surface.

Maxilliped (Fig. 80).—Ischion distinct, with 2 short spines on its ventral surface. Remainder of endopodite subtriangular in outline with divisions between its 4 articles indicated by lobes on inner margin and by oblique suture lines between these. Each lobe bears a tuft of coarse setae. There are 2 spines on outer margin of endopodite. Endite subconical with a blunt apex; its inner surface setose. On apex of endite are a large, conical, setose process and a short spine situated to outer side of process. With setose process excluded, endite does not extend beyond basal lobe of endopodite.

Pereion.—Posterior borders of 1st–4th segments almost straight with angles rounded. Epimera of 5th segment directed slightly backwards; their posterior borders curved outwards and posterior angles subacute. Epimera of 6th and 7th segments directed more sharply backwards, also with posterior angles subacute. On ventral surface, epimera of 1st–3rd segments (Fig. 81) each exhibit a thick ridge. Lateral margins of segments bordered with short spines (Fig. 82) each consisting of a partially divided outer sheath and a central clubbed seta. Such spines also occur on dorsal surface of epimera, but no spines on central part of segments. Dorsal surface has covering of rounded scales and also bears small scattered scale-setae.

Pereiopods.—Large spines on 1st leg each consist of a partially divided outer sheath and a central clubbed seta. They are of two types; larger spines with almost half length of outer sheath split, and smaller spines with splits beginning only near apex of sheath. Dactylos ends in a simple claw. Basal third of dactylar seta subcylindrical, lacking secondary setae. Remainder of dactylar seta broader than basal part, and slightly flattened, having a sharply rounded apex, and densely covered with fine setae. Dactylos of 2nd leg shown in Figure 83. Seventh leg well-developed but slightly shorter than remainder; lengths: 1st leg 2·5 mm, 6th leg 2·6 mm, 7th leg 2·3 mm.

Male organ (Fig. 84).—Basal three-quarters of male organ forms a broad oval expansion, beyond which projects a narrower distal quarter having straight sides and a truncate apex. On dorsal surface, centre of oval region is raised above its sides, limits of this thicker portion being continuous with lateral margins of distal quarter. The two ducts remain distinct and open separately into a hollow in apex of organ.

Pleon (Fig. 85).—Semicircular; its lateral borders continuous with those of pereion. Pleura of 3rd–5th segments bent backwards; 3rd pleura narrow and acute with a few spines at apex; 4th and 5th pleura large with posterolateral margins

rounded and bordered with spines. A few spines also present on both surfaces of these pleura, but no spines on central part of segments. Terminal segment subtriangular with apex very sharply rounded. Tergites bear scales and scale-setae like those on pereion.

First pleopod (Fig. 86).—Exopodite suboval with anterior and posterior borders indented. On its dorsal surface are 2 thickened bands beginning at outer edge; one follows anterior border and the other crosses centre of exopodite. Endopodite styliform and grooved along its length, with groove beginning on inner surface at its base and twisting on to dorsal surface nearer apex; edges of distal half of groove bear short setae.

Second pleopod (Fig. 87).—Protopodite a narrow bar with its outer side produced into a small lobe. Exopodite irregularly 4-sided with anterior border nearly straight, lateral borders curved outwards, and posterior border indented on inner side; inner posterior angle bluntly rounded. There is a large seta on posterior border. An oblique band of thickening on dorsal surface begins at outer anterior angle. Endopodite suspended from inner side of protopodite; it is styliform and curved outwards; there is a chitinous thickening down greater part of its inner surface. Endopodite not divided into 2 articles, although such a division is indicated by a faint oblique suture line corresponding with a sudden decrease in width of endopodite. Ventral surface of basal part raised into a curved ridge.

Third pleopod (Fig. 88).—Shape of exopodite similar to that of 2nd exopodite, in particular inner posterior angle bluntly rounded. There are short setae on inner border and 2 large setae on posterior border.

Uropod (Figs. 85, 89).—Protopodite projects beyond terminal segment; its outer region produced backwards to form a broad lobe. Margin of lobe rounded, slightly crenate, and bearing spines similar to those on lateral borders of pereion; such spines also scattered over both surfaces of lobe. Inner margin of protopodite incised near its base. Exopodite subcylindrical and inserted on dorsal surface of protopodite, near its posterior margin, to inner side of lobe, beyond which it projects for a short distance. Endopodite narrowly conical and inserted on ventral surface of protopodite at its inner basal corner. On ventral surface, inner side of protopodite is deeply indented to form a groove to receive endopodite. Protopodite longer than broad. Maximum length of protopodite 0·62 mm, breadth 0·43 mm; length of rami: exopodite 0·27 mm, endopodite 0·48 mm.

Female

Length of largest specimen 5·6 mm, breadth 2·8 mm. Female differs from male in the following structures:

First pleopod.—Endopodite not developed.

Second pleopod (Fig. 90).—Endopodite conical with apex bluntly rounded; it is almost same length as exopodite.

Habitat

Description is based on specimens found enrolled in burrows in the sand, under pieces of seaweed, or walking on the beach near the edge of the incoming

tide, at Pirates' Bay, Eaglehawk Neck, on 3.v.1957; 33 males and 38 females obtained. Other specimens were found on beaches at Marion Bay, Seven Mile Beach, Clifton Beach, Roaring Beach (South Arm), and Hawley.

Variations

Some specimens from Clifton Beach are a larger size than maximum noted from Eaglehawk Neck. Length of largest male specimen from Clifton Beach 7·0 mm; length of largest female 7·3 mm.

In one male specimen from Eaglehawk Neck outer lobe of each 1st maxilla has only 1 bifid tooth, this being 2nd innermost tooth on left appendage and 5th innermost tooth on right appendage.

Remarks

Dana (1853, p. 735) described the flagellum of the 2nd antenna in *A. euchroa* as indistinctly 5- or 6-jointed. Probably the indentations in the 2nd and 3rd articles of the flagellum might have been mistaken for divisions between articles.

Thomson (1893) described and figured (pl. 2, fig. 3) the 1st antenna as having 2 articles instead of 3; however, the distal articulation in this appendage might easily have been overlooked. His description and figure (fig. 5) of "the mandibles" apply only to the left mandible. As was noted by Chilton (1901, p. 131), the structure which Thomson described and figured (fig. 6) as the inner lobe of the 1st maxilla was actually the 2nd maxilla. Thomson stated that the lateral portions of the 3rd, 4th, and 5th segments of the pleon have their margins rounded; this is true of the 4th and 5th segments, but the pleura of the 3rd segment are acute. The apex of the terminal segment is more sharply rounded than Thomson figured it (fig. 8).

Chilton (1901, p. 132) described the endopodite of the 2nd male pleopod of *A. euchroa* as 2-jointed, whereas in my specimens it is not distinctly divided into 2 articles, but from his drawing (pl. 15, fig. 3, plp. 2♂) of this structure it appears that he considered the protopodite as one article.

The ocelli of the eye in my specimens are not "very numerous" as was noted by Chilton (p. 131) in his description of New Zealand examples of *A. euchroa*. Also the eyes themselves are smaller and more rounded than those figured for *A. euchroa* by Chilton (pl. 15, fig. 3) and Jackson (1928, fig. 10). However, the eyes are comparable in size and shape to those of a specimen from Eaglehawk Neck figured by Thomson (pl. 2, fig. 1). Chilton (p. 130) made use of such a difference in the size of the eyes in distinguishing *A. opihensis* Chilton, 1901, from *A. euchroa*. From this it might appear that the Tasmanian specimens should also be considered as specifically distinct from the New Zealand examples of *A. euchroa*. However, as Chilton (p. 101) noted the occurrence in Tasmania of *A. euchroa* and (p. 130) included a reference to Thomson's (1893) description in his bibliography of this species, it is evident that he accepted Thomson's identification of his specimens from Eaglehawk Neck as *A. euchroa*. As Chilton (p. 99) claimed to have had the whole of Thomson's collection it is possible that he had the opportunity to actually examine these specimens. My Tasmanian specimens agree

with those from New Zealand described by Chilton in characters other than those of the eyes. In this paper I therefore follow Thomson (1893) in identifying specimens of *Actaecia* from Eaglehawk Neck as *A. euchroa,* but note that the Tasmanian representatives of this species probably constitute a distinct variant of the New Zealand form.

Actaecia pallida Nicholls & Barnes

Figs. 91–100

Actaecia pallida Nicholls and Barnes, 1927, p. 155, text-fig. 2, pl. 20.

The Tasmanian specimens which I consider may be assigned to *A. pallida* differ in a few details from the Western Australian specimens described by Nicholls and Barnes. The following account of my Tasmanian material is therefore given for comparison.

Male

Size.—Length of largest specimen 4·4 mm, breadth 2·2 mm.

Colour.—As described for *A. euchroa.*

Cephalon.—Maxillipedal somite distinct. Vertex bears scattered simple spines. Frontal line forms a sharp ridge, slightly depressed in centre, and edged with spines. A V-shaped ridge on frons possibly represents supra-antennal line. Antennary tubercles not developed. Eyes oval, each composed of 14–18 ocelli.

First antenna.—Third article bears 2 apical setae.

Second antenna.—Length of peduncle 1·70 mm; length of flagellum 0·33 mm. Spines on antenna as described for *A. euchroa.* Flagellum has 4 articles. Length of 4th article (Fig. 91) not more than twice its greatest breadth; length: 0·0525 mm, breadth 0·0300 mm.

Mandibles.—Lacinia mobilis of right mandible (Fig. 92) ends in a mushroom-shaped structure bearing numerous, small, tooth-like processes. In other respects, including structure of molar portion, mandibles as described for *A. euchroa.*

First and 2nd maxillae.—As described for *A. euchroa.*

Maxilliped (Fig. 93).—On ventral surface of lobe representing meros, near its inner margin, and below its tuft of coarse setae, is a dense tuft of fine setae. With its setose process excluded, endite scarcely extends beyond basal lobe of endopodite. Otherwise maxilliped as described for *A. euchroa.*

Pereion.—Shape of epimera, and ridges on ventral surface of 1st–3rd segments, as described for *A. euchroa.* Lateral margins of segments bordered with short spines, each consisting of an outer sheath, split near the end into several short points, surrounding a seta, clubbed at its apex. Narrower simple spines scattered over dorsal surface of pereion, which also has covering of rounded scales.

Pereiopods.—Spines and claw of 1st leg as described for *A. euchroa.* Basal third of dactylar seta (Fig. 94) lacks secondary setae. Its distal two-thirds are broader than basal third, slightly flattened, and have a dense covering of short

Figs. 91-100.—*Actaecia pallida* Nicholls & Barnes: *91*, terminal article of flagellum of left 2nd antenna, ventral view; *92*, distal part of right mandible, dorsal view; *93*, distal part of left maxilliped, ventral view; *94*, dactylos of left 1st leg, anterior view; *95*, seventh segment of pereion, pleon, and uropods, dorsal view; *96*, left 1st pleopod of male, dorsal view; *97*, right 2nd pleopod of male, ventral view; *98*, right 3rd pleopod of male, ventral view; *99*, left uropod, dorsal view; *100*, left 2nd pleopod of female, dorsal view.

setae; a long fine seta is set on anterior side at base of broader setose portion. Apex of dactylar seta sharply rounded. Lengths of legs: 1st leg 1·80 mm, 6th leg 1·9? mm, 7th leg 1·78 mm.

Male organ.—As described for *A. euchroa*.

Pleon (Fig. 95).—Semicircular; its lateral borders continuous with those of pereion. Pleura of 3rd–5th segments curved backwards, those of 3rd segment narrow and acute, those of 4th and 5th segments subrectangular with posterolateral borders straight. Terminal segment triangular with apex sharply rounded. Spines, like those on lateral borders of pereion, present on apices of 3rd pleura and along posterolateral borders of 4th and 5th pleura. Dorsal surface of segments bears rounded scales and simple spines.

First pleopod (Fig. 96).—Exopodite suboval, with anterior and posterior borders indented. On its dorsal surface, a thickened band extends from outer side across centre of exopodite. Endopodite styliform and grooved along its length, with groove beginning on inner surface and twisting on to dorsal surface. Near apex, outer edge of groove is bordered with setae.

Second pleopod (Fig. 97).—Protopodite a narrow bar; its outer side produced into a small lobe. Exopodite subrectangular with posterior border indented; its inner posterior angle forms a rounded right angle. An oblique band of thickening on dorsal surface of exopodite begins at outer anterior angle. There is a large seta on posterior border of exopodite. Endopodite suspended from inner region of protopodite; it is styliform, and has a chitinous thickening down greater part of its inner surface. Endopodite not divided into 2 articles, but a sudden decrease in width near its base probably indicates that 2 articles are represented. Ventral surface of basal region raised into a curved ridge.

Third pleopod (Fig. 98).—Exopodite subrectangular with posterior border indented; its inner posterior angle subacute, bearing a long seta; another such seta on posterior border. Inner border fringed with short setae.

Fourth and fifth pleopods.—Distribution of setae on exopodites like that on 3rd exopodite.

Uropod (Figs. 95, 99).—Protopodite projects beyond terminal segment. It is subrectangular with posterior border, to outer side of exopodite, nearly straight except for slight crenulations, and forming a distinct angle with outer border. Inner border incised. Posterior border edged with spines like those on lateral borders of pereion, and a few simple spines present on both surfaces of protopodite. Exopodite subcylindrical and inserted on dorsal surface of protopodite, near its inner posterior angle; it projects a little beyond protopodite. Endopodite narrowly conical and inserted on ventral surface of protopodite at its inner basal angle. On ventral surface, inner side of protopodite deeply indented to form a groove to receive endopodite. Protopodite a little broader than long. Maximum length of protopodite 0·30 mm, breadth 0·32 mm; length of rami: exopodite 0·12 mm, endopodite 0·23 mm.

Female

Length of largest specimen 4·8 mm, breadth 2·4 mm. Female differs from male in the following structures:

First pleopod.—Endopodite not developed.

Second pleopod (Fig. 100).—Exopodite subrectangular with posterior border indented, bearing a long seta, and inner posterior angle subacute, also bearing a seta. Endopodite conical with apex sharply rounded; it is a little longer than exopodite.

Habitat

Description is based on specimens found under seaweed on a beach at Hawley, on 19.ii.1958; 69 males and 67 females obtained. Other specimens were found on beaches at Eaglehawk Neck, Dodge's Ferry, Seven Mile Beach, Clifton Beach, Roaring Beach (South Arm), and Adventure Bay, Bruny I.

Remarks

Nicholls and Barnes (p. 155, pl. 20, fig. 2) described and drew the terminal article of the flagellum of the 2nd antenna in *A. pallida* as being more than twice as long as it is broad. In my specimens, if the apical tuft of setae is not included in the measurement, the length of this article is just twice its greatest breadth, or less. In the left 2nd antennae of 10 male specimens from Hawley the ratio of length to breadth of the terminal article has been found to vary from 1·75 (length 0·0525 mm; breadth 0·0300 mm) to 2·00 (length 0·0550 mm; breadth 0·0275 mm), measurements being made using a 10× micrometer eyepiece and a 65× objective lens.

The molar portion of the mandible was described (p. 155) and figured (pl. 20, figs. 13, 14) as consisting of a very long bushy seta. In my specimens the distal end of the molar tubercle forms an axis on which separate plumose setae are set at different levels; the pencil so formed being less compact than those figured by Nicholls and Barnes.

Nicholls and Barnes (pl. 20, fig. 1) showed the pleura of the 3rd segment of the pleon as being subrectangular, like those of the 4th and 5th segments, whereas in my specimens the 3rd pleura are triangular and acute.

The endopodite of the 2nd pleopod in my male specimens is not clearly divided into 2 articles; however, it would appear from the description (p. 157) and figure (text-fig. 2*b*) of the 2nd male pleopod given by Nicholls and Barnes that they considered the protopodite as one article. They stated that there were no setae present on margins of exopodites of pleopods. In my specimens the 2nd–5th exopodites exhibit setae, although these might easily be overlooked.

However, as in other respects, particularly with regard to the shape of the uropods, the characters of my specimens from Hawley are in close agreement with those described for *A. pallida* by Nicholls and Barnes, I am satisfied that the Tasmanian specimens should be assigned to this species.

VIII. Family **ONISCIDAE**

Genus PLYMOPHILOSCIA Wahrberg

Plymophiloscia Wahrberg, 1922, p. 101.

Type species *Philoscia* (*Plymophiloscia*) *maxima* Wahrberg, 1922.

Wahrberg established *Plymophiloscia* as a subgenus of genus *Philoscia* Latreille, 1804, and placed in it two new species, *Ph.* (*Pl.*) *maxima* and *Ph.* (*Pl.*) *guttata*, both from Queensland. He did not specifically designate either of these species as the type, and I have found no reference to any subsequent selection of a type species for *Plymophiloscia*. However, Wahrberg used some characters of *Ph.* (*Pl.*) *maxima*, which has page precedence, as a standard for comparison in describing *Ph.* (*Pl.*) *guttata*. I therefore nominate *Philsocia* (*Plymophiloscia*) *maxima* Wahrberg, 1922, as the type species of *Plymophiloscia* Wahrberg, 1922.

Generic Diagnosis

Wahrberg's (p. 101) provisional definition of *Plymophiloscia*, based entirely on characters of the mouthparts, was as follows (translated from the original German):

"Mandibles: Left mandible: pencils 1 + 2. Right mandible: pencils 1 + 1. Inferior seta with short radix and many main branches, robust.

First maxillae: Teeth 4 + 6. The inner teeth are 2-pointed, with the exception of the 5th, which is one-pointed and shorter than the remainder. Interior lacinia: 2 long pencils.

Second maxillae: The inner lobe well distinguished from the outer and somewhat higher, yet narrower. Inner lobe densely set with rather coarse setae. Inner side of the outer lobe with especially fine hair-setae, which stand in groups.

Maxillipeds: Endite with long spine and two small teeth on the outer, upper border. In the inner angle a small pencil. Upper part of the endite densely set with fine setae, which stand in groups of 2 or 3. Endopodite longer than endite. Only the basal article is clearly distinguished and is armed with 2 strong setae. The remaining part with 3 projecting collections of setae, which indicate 3 fused articles. In the apical group of these collections of setae and that situated next below it the number of setae approaches many. In the lowest group in comparison are found only 2, a stronger one and a weaker one. Distal part of basipodite rounded, with long, fine hair-setae, which stand in groups."

This definition separates *Plymophiloscia* from *Philoscia* Latreille, 1804, Verhoeff, 1908, s.s., in which the endite of the maxilliped has no setae or pencil.

Verhoeff (1926) classed *Plymophiloscia* as a genus, and (p. 323) distinguished it from other genera of Oniscidae from the Australian region by means of a key in which he introduced other characters beside those of the mouthparts. The characters which Verhoeff thus attributed to *Plymophiloscia* were as follows:

Frontal line of cephalon absent. Inner teeth on outer lobe of 1st maxilla curved inwards and mostly (usually 5 of 6) split at the end; no middle teeth on this lobe. Endite of maxilliped setose with a cone at apex and 2 small teeth on outer angle. First to 3rd tergites have posterior borders rounded or transverse, with posterior angles not drawn out into lobes, or, if lateral indentations do occur, they are shallow and confined to posterior borders of epimera. Posterior border of 4th tergite bent out on each side, with posterior angles projecting as short triangles. Epimeral glands open in a row along lateral borders of epimera. Dorsal surface not tuberculate and lacking seta-scales ("Borstenschuppen"); it may exhibit scale structure ("Schuppenstruktur") but this is absent from lateral borders of segments. If scale-setae ("Schuppenborsten") occur they do not take the form of oval clubs or short stalks. Pleura of 3rd–5th segments of pleon well developed, not or only slightly bent downwards, and thus completely visible in dorsal view.

Verhoeff (1926, p. 334) placed in *Plymophiloscia* a new species, *Pl. montana*, from New Caledonia.

I have collected examples of four species which belong in *Philoscia* Latreille according to the diagnosis given by Sars (1899, p. 172). These may be further placed in *Plymophiloscia* according to Wahrberg's definition. However, they do not conform in all respects to Verhoeff's characterization of *Plymophiloscia*. In all of my species a frontal line is indeed absent in the middle region of the cephalon, but it is represented on each side as a ridge in front of the eye. In all four species the outer lobe of the 1st maxilla does exhibit 2 tooth-like spines (middle teeth) near the base of the 4th large tooth; however, these are inconspicuous and might be overlooked. The posterior angles of the 4th segment of the pereion are angular and very slightly drawn backwards in one of my species (*Pl. notleyensis*), but in the other three they form rounded right angles and the posterior border of the 4th segment is more nearly transverse.

In sections G and H of his key, Verhoeff used the characters of the 4th segment of the pereion, and also those of the 3rd–5th pleura of the pleon, as a contrast between *Wahrbergia* Verhoeff, 1926, and *Plymophiloscia* on one hand and *Laevophiloscia* Wahrberg, 1922, and *Heroldia* Verhoeff, 1926, on the other hand. In *Laevophiloscia* and *Heroldia* the posterior border of the 4th segment is transverse with the posterior angles rounded, and the 3rd–5th pleura are poorly developed and more or less strongly bent downwards, so that they are either not visible from above or only their terminal points are still visible. Thus, while all of my species agree with *Wahrbergia* and *Plymophiloscia* in having the 3rd–5th pleura completely visible, three of the four species agree with *Laevophiloscia* and *Heroldia* in the form of the 4th segment of the pereion.

Within section G the Tasmanian species are excluded from *Wahrbergia* and agree with *Plymophiloscia* as they have a non-tuberculate dorsal surface, exhibit epimeral gland pores, and have 2 small teeth on the outer angle of the endite of the maxilliped. Within section H they are excluded from *Laevophiloscia* and agree with *Heroldia* as the endite of the maxilliped is setose, indented at the apex, and has a small setose cone on the inner side; also the endopodite of the maxilliped has a pencil-like group of setae ("Nebengriffel") on its inner border. Verhoeff (1928, p. 218) later identified *Laevophiloscia* as a synonym of *Chaetophiloscia* Verhoeff, 1908, to which the same distinction applies. Thus, according to Verhoeff's (1926) key, one of my species belongs in *Plymophiloscia* while the other three occupy a position between *Plymophiloscia* and *Heroldia*. But the difference in the form of the 4th segment in the one species (*Pl. notleyensis*) from that in the other three species is only one of degree. Also the former species is closer to two of the others (*Pl. thomsoni* and *Pl. tasmaniensis*) in other characters, such as the number of epimeral gland pores, the ornamentation of the 1st–3rd legs of the male, and the shape of the endopodite of the 1st pleopod of the male, than is the remaining species in which the angles of the 4th segment are rounded (*Pl. ulverstonensis*). I therefore assign all four species to *Plymophiloscia*, regardless of Verhoeff's restriction on the 4th segment of the pereion. With this character excluded from

the limits of the genus, *Heroldia* is still narrowly separated from *Plymophiloscia*, according to Verhoeff's (1926) key, on the form of the pleon.

Status of Plymophiloscia

Van Name (1936, p. 112) considered that, in many cases, the treatment of sections of *Philoscia* Latreille as full genera involved losing sight of important resemblances and relationships in the effort to emphasize small differences. He therefore regarded such sections as subgenera of *Philoscia*, s.l. Jackson (1941, p. 2) agreed with Van Name (p. 12); he returned *Plymophiloscia* to the status of a subgenus of *Philoscia* Latreille and likewise classed *Chaetophiloscia, Heroldia,* and *Wahrbergia* as subgenera of *Philoscia*. I consider that the limits of many of the subdivisions of *Philoscia*, s.l. are too narrow; the position of the Tasmanian species is an example of this. However, as *Philoscia*, s.l. is one of the largest genera of terrestrial isopods, I feel that some division into smaller genera is desirable.

Verhoeff (1926, p. 333) suggested that *Plymophiloscia* and *Wahrbergia* should perhaps be combined as subgenera of one genus. The position of the Tasmanian species indicates that *Heroldia* should probably be united with *Plymophiloscia*. Verhoeff (1928, p. 218) recognized *Laevophiloscia* as a synonym of *Chaetophiloscia* and suggested that *Heroldia* should perhaps be regarded as a subgenus of *Chaetophiloscia*. Herold (1931, p. 374) considered his new genus *Leptophiloscia* to belong between *Laevophiloscia* and *Heroldia*. It seems likely that the present systems of classification of species in the *Philoscia* group might be improved if some of these, and perhaps other related sections, were to be combined to form genera intermediate in size between *Philoscia*, s.l. and its present subdivisions. However, such a step should not be taken without a comprehensive study of examples of the sections concerned. In the present paper I therefore accept the limits of *Plymophiloscia* imposed by Wahrberg and Verhoeff except as regards those characters of the cephalon, 1st maxilla, and 4th segment of the pereion which have already been discussed.

My species are distinct from those already placed in *Plymophiloscia*. A check on species from the Pacific region which have simply been placed in *Philoscia*, s.l. shows that these are either excluded from *Plymophiloscia* on characters of the mouthparts, or have been too inadequately described to be assigned to a subdivision of the *Philoscia* group. The Tasmanian species are therefore regarded as new. Their distinction from the established species of *Plymophiloscia* and from each other is demonstrated in the following key.

KEY TO SPECIES OF THE GENUS PLYMOPHILOSCIA

1. Body narrow; ratio of its length : breadth at least 3·3 : 1 ..... *guttata*
   Body broader; ratio of its length : breadth less than 2·5 : 1 2
2. Outer lobe of 1st maxilla with 9 teeth; pereion with scales restricted to epimera .. *montana*
   Outer lobe of 1st maxilla with 10 teeth; pereion with scales over its entire dorsal surface 3
3. Endopodite and exopodite of uropod articulated at about the same level on protopodite ..... *maxima*
   Endopodite of uropod articulated on protopodite distinctly anterior to exopodite 4

4. Number of gland pores on each epimeron small (3–6); endopodite of 1st pleopod of male styliform and evenly tapering to a straight, pointed apex ..... *ulverstonensis*, sp. nov.
   Number of gland pores on each epimeron larger (13 or more); endopodite of 1st pleopod of male club-shaped and not evenly tapering, with its apical region not forming a straight point 5
5. Posterior angle of 4th segment of pereion forming a definite right angle; 1st leg of male with propodos subcylindrical, not broadened dorsoventrally; endopodite of 1st pleopod of male with its apical region forming an outwardly directed, triangular lobe ..... *notleyensis*, sp. nov.
   Posterior angle of 4th segment of pereion forming a rounded right angle; 1st leg of male with propodos broadened dorsoventrally and oval in outline; endopodite of 1st pleopod of male with its apical region not formed of such a lobe 6
6. Exopodite of 1st pleopod of male with its outer border curved outwards; endopodite of 1st pleopod of male exhibiting on its outer side a protuberance covered with elongated conical processes; exopodite of 1st pleopod of female with its outer border scarcely incurved and its apex bluntly rounded ..... *tasmaniensis*, sp. nov.
   Exopodite of 1st pleopod of male with its outer border curved inwards; apical region of endopodite of 1st pleopod of male exhibiting short papillate processes; exopodite of 1st pleopod of female with its outer border distinctly incurved and its apex sharply rounded ..... *thomsoni*, sp. nov.

Plymophiloscia thomsoni, sp. nov.

Figs. 101–118

Oniscus punctatus Thomson, 1893, p. 54, pl. 1, figs. 6-13 (non Thomson, 1879).

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male

Size.—Length of largest specimen 6·5 mm, breadth 3·1 mm.

Colour.—In live specimen, background colour of dorsal surface medium brown except for 3 longitudinal bands of dark brown on pereion, one in mid-line and one on each side above bases of epimera, and for a band of dark brown down each side of pleon. Each dark band on pereion marked by a row of unpigmented patches. Large unpigmented patches on epimera together form another row of spots down each side of pereion. Cephalon, areas between dark bands on pereion, and middle region of pleon mottled with irregular unpigmented patches.

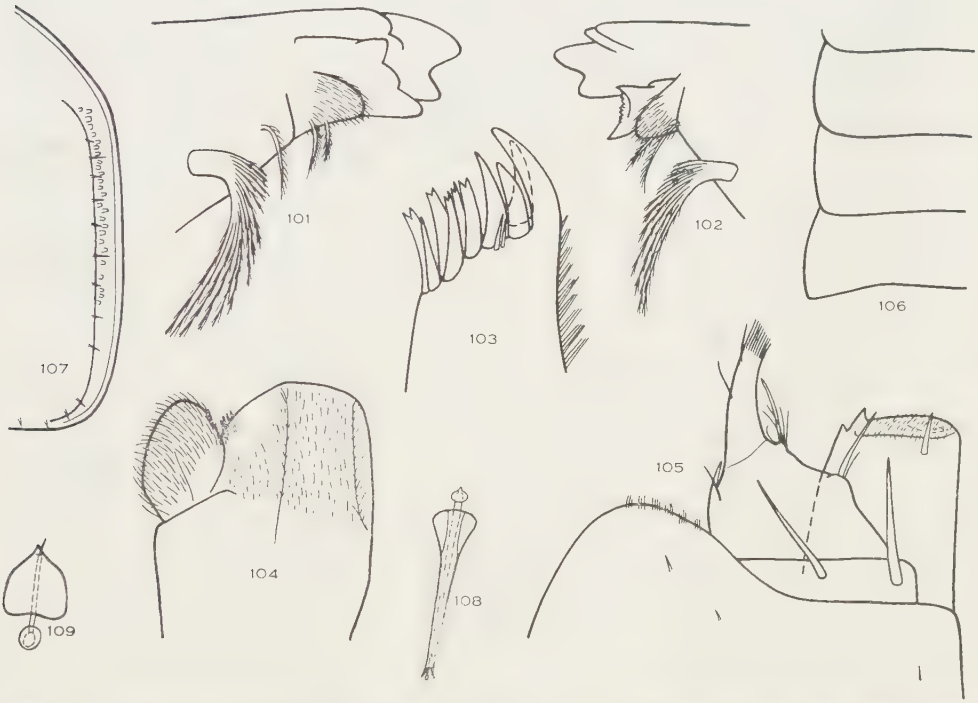
Cephalon.—Surface of vertex smooth. Frontal line not developed across middle of cephalon, but at sides evident as a ridge in front of each eye. Supra-antennal line present. Antennary tubercles small, not visible in dorsal view. Eyes oval, each composed of 20–23 ocelli.

First antenna.—Triarticulate; 3rd article conical with a group of setae on inner surface and 2 long setae on apex.

Second antenna.—Length of peduncle 3·20 mm; length of articles of flagellum: 1st 0·40 mm, 2nd 0·32 mm, 3rd 0·47 mm. All articles of antenna bear rows of spines. Third article of flagellum ends in a process formed of partly fused setae.

Left mandible (Fig. 101).—Incisor process consists of a bifid tooth and a smaller simple tooth, the 2 teeth joined by a ridge. Lacinia mobilis ends in 3 teeth. Setose lobe bears 2 pencils of setae; 1 pencil behind lobe. Molar portion represented by a tuft of plumose setae set on a common basal process.

Right mandible (Fig. 102).—Incisor process consists of a bifid tooth and 2 simple teeth. Apex of lacinia mobilis has a pointed process on each side and uneven ridges between the 2 processes. One pencil of setae on setose lobe and 1 pencil behind lobe. Molar portion like that of left mandible.



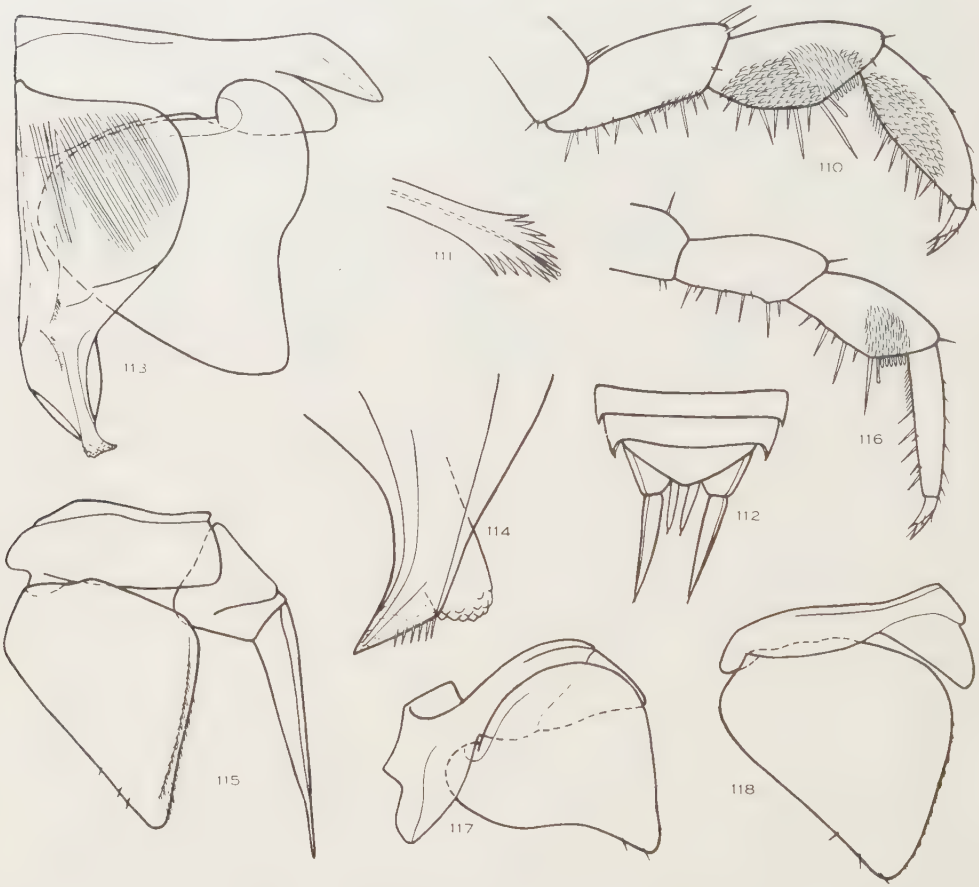
Figs. 101–109.—*Plymophiloscia thomsoni,* sp. nov.: *101,* distal part of left mandible, dorsal view; *102,* distal part of right mandible, dorsal view; *103,* distal part of outer lobe of left 1st maxilla, ventral view; *104,* distal part of left 2nd maxilla, ventral view; *105,* distal part of right maxilliped, ventral view; *106,* left epimera of 3rd–5th segments of pereion, dorsolateral view; *107,* right epimeron of 4th segment of pereion, dorsal view, showing gland pores; *108,* spine on posterior border of 1st segment of pereion, dorsal view; *109,* scale-seta on lateral border of 1st segment of pereion, dorsal view.

First maxilla.—Outer lobe (Fig. 103) ends in 10 teeth forming an outer group of 4 simple teeth and an inner group of 6 teeth, of which 5th is simple and rest are bifid. On ventral surface are 2 spines near base of 4th simple tooth. Inner lobe bears 2 thick setose processes; there is a small spine on outer side of lobe.

Second maxilla (Fig. 104).—Apex of maxilla divided into 2 subrectangular lobes. Base of inner lobe defined by a suture line. Distal region of inner lobe has dense covering of setae; that of outer lobe, except for a clear area in inner

angle, covered with finer setae. A few long coarse setae project into notch between lobes.

Maxilliped (Fig. 105).—Outer side of basis produced beyond base of endopodite as a rounded lobe with comb-setae on margin. Ischion distinct; 2 very



Figs. 110–118.—*Plymophiloscia thomsoni*, sp. nov.: *110*, distal part of left 1st leg of male, anterior view; *111*, distal part of spine on under surface, nearest distal end of carpos, of left 1st leg of male, anterior view; *112*, fourth, 5th, and terminal segments of pleon and uropods, dorsal view; *113*, right 1st pleopod of male, dorsal view; *114*, distal part of endopodite of right 1st pleopod of male, ventral view (position of papillae on dorsal surface indicated by dots); *115*, right 2nd pleopod of male, ventral view; *116*, distal part of left 1st leg of female, anterior view; *117*, right 1st pleopod of female, ventral view; *118*, right 2nd pleopod of female, ventral view.

long spines on its ventral surface. Division of remainder of endopodite into 2 articles indicated by a faint suture line. There are 2 groups of setae on inner border of first of these articles; basal set consists of 1 large and 1 smaller seta, distal set of 1 large seta and 5–7 smaller setae. Three setae occur singly on outer border of endopodite; near base of lowest one is a pencil which itself lacks setae. Endopodite

ends in a tuft of setae. Endite subquadrangular with a transverse indentation in ventral surface near its apex. It has a spine on inner side behind indentation, 2 small teeth on outer apical corner, and a small conical process, bearing a few coarse setae, set in an indentation in dorsal surface near inner apical corner. Apical region of endite bears very short, scattered setae.

Pereion.—Posterior borders of 1st–4th segments almost straight; posterior angles of 1st–3rd segments bluntly rounded, those of 4th segment right-angled and rounded. Epimera of 3rd–5th segments illustrated (Fig. 106). Epimera of 5th–7th segments directed backwards with posterior angles subacute. Seventh epimera do not extend back beyond 4th segment of pleon. Dorsal surface of pereion smooth, except for a longitudinal groove near lateral border of each epimeron. Number of gland pores opening into each groove ranges from 20 to 29. Pores more numerous in anterior third, fewer in middle third, and absent from posterior third of groove. There is a row of spines above inner edge of groove. Epimeron of 4th segment illustrated (Fig. 107). Tergites have covering of scales and also bear long, scattered spines. One such spine (Fig. 108) consists of a central seta surrounded by a sheath, basal part of which is expanded on each side. Scale-setae present on lower edge of lateral borders of segments. Scale portion of one of these scale-setae (Fig. 109) broad and subtriangular with sides curved out and apex sharply pointed.

Pereiopods.—Carpos and propodos of 1st leg (Fig. 110) broadened dorso-ventrally; as a result, lower border of carpos curved outwards and propodos oval in outline. Most of spines on leg each consist of a central seta and an outer sheath, apex of which is divided into 3 or 4 points. Spine nearest distal end of carpos (Fig. 111) has sheath divided into at least 12 points placed symmetrically on each side of its central seta. Spines on under surface of meros and carpos too scattered to appear as a brush. Spatulate scales occur on under surface of carpos, near its distal end; an area on anterior surface above them covered with long setae. Short simple spines occur on under surface of propodos. Areas covered by large, projecting, backwardly sloping scales present on under surface of meros and anterior surface of carpos and propodos. Dactylos has terminal claw and accessory claw.

Carpos and propodos of 2nd leg broadened but to a lesser degree than those of 1st leg. In 3rd–7th legs these articles narrower; their upper and lower borders not curved. Multipointed spine, spatulate scales and area of setae at distal end of carpos, and simple spines on under surface of propodos not repeated on 2nd–7th legs. Areas covered by large backwardly sloping scales occur on meros, carpos, and propodos of 2nd leg and carpos of 3rd leg.

Male organ.—Conical in outline with apex subacute. Its 2 ducts remain separate and open under a flap on its dorsal surface.

Pleon.—Length (along mid-line) 1·50 mm, breadth (across 3rd segment) 1·65 mm. Pleon abruptly narrower than pereion. Pleura of 3rd–5th segments very small, acute, and produced backwards, visible in dorsal view (see Fig. 112). Terminal segment (Fig. 112) triangular with lateral borders not incurved and apex

bluntly rounded. Dorsal surface of pleon smooth. Tergites bear scales and spines like those on pereion, but have no scale-setae on lateral borders.

First pleopod (Fig. 113).—Exopodite subtriangular with outer border shallowly indented and apex sharply rounded; its anterior border exhibits a fold near outer angle. Endopodite club-shaped with distal third bent outwards. Dorsal surface of endopodite exhibits irregular ridges, some ornamented with scales and setae. A broad, oval, chitinous thickening occurs on both inner and outer border of distal third. Apex of endopodite (Fig. 114) folded and irregular in shape, with inner angle rounded and outer angle acute. Its dorsal surface raised into papillate processes. On ventral surface, inner side of apex is rounded and papillate, while outer side forms a trapezoidal lobe which, due to folding of endopodite, lies ventral to rounded inner part. Ventral surface of this outer lobe exhibits ridges but lacks papillae; posterior border of lobe bears a row of spines.

Second pleopod (Fig. 115).—Exopodite triangular with outer border almost straight and apex sharply rounded. Comb-setae present on its inner border and on ridges near border; spines on outer border near apex. Length of articles of endopodite: 1st 0·43 mm, 2nd 0·93 mm. First article quadrangular in outline; 2nd article styliform, with a broad chitinous thickening down inner edge of its basal three-quarters, beyond which article becomes very narrow and flagelliform. Length of flagelliform portion 0·25 mm.

Third pleopod.—Exopodite subquadrangular with posterior border almost straight and apex sharply rounded.

Uropod (Fig. 112).— Protopodite extends beyond apex of terminal segment for about one-fifth of its own length; it has a groove down outer surface. Insertion of endopodite anterior to that of exopodite; distance separating insertions of exopodite and endopodite 0·15 mm. Rami conical. There is a groove down outer surface of exopodite and another down inner surface of endopodite. Greatest length of protopodite 0·55 mm; length of rami: exopodite 0·98 mm, endopodite 0·52 mm.

Female

Length of largest specimen 8·4 mm, breadth 3·7 mm. Female differs from male in the following structures:

Pereiopods.—Carpos and propodos of 1st and 2nd legs not broadened dorsoventrally. (First leg shown in Fig. 116.) No areas of large backwardly sloping scales on meros, carpos, or propodos of 1st–3rd legs.

First pleopod (Fig. 117).—Exopodite subtriangular with outer border shallowly indented, although indentation more pronounced than in 1st exopodite of male, and apex sharply rounded; anterior border exhibits a fold near outer angle. Endopodite not developed.

Second pleopod (Fig. 118).—Exopodite triangular with outer border straight and apex more bluntly rounded than that of 2nd exopodite of male. A subtriangular lobe, projecting back from inner side of protopodite, possibly represents an endopodite.

Third pleopod.—Apex of exopodite more bluntly rounded than in 3rd pleopod of male.

Habitat

Type locality.—Description is based on specimens found in debris and under wood and stones on the ground at altitudes of 2700–4100 ft on Mt. Wellington; collections made were as follows: 15.v.1956, 31 specimens; 17.x.1956, 6 specimens; 22.x.1956, 8 specimens; 28.v.1957, 20 specimens; a total of 23 males and 42 females.

Other localities.—Specimens were found in debris and under logs in a forest of eucalypts and tree ferns at Tarraleah.

Variations

Intensity of brown pigmentation varies, so that in some specimens background colour of dorsal surface is almost uniformly dark. Some specimens exhibit orange-brown pigmentation which replaces the true brown on dorsal surface completely, or everywhere except for the dark brown bands on pereion and pleon, or only on epimera and pleura.

Remarks

Thomson (1893, p. 54) described specimens collected on Mt. Wellington and assigned them to *Oniscus punctatus* Thomson, 1879, a species which he (1879, p. 232) established on material from Dunedin, N.Z. Chilton (1901, p. 134) noted that these Tasmanian specimens differed from New Zealand specimens of *O. punctatus* in having the 3rd–5th pleura much smaller, and suggested that the former should perhaps be placed in *Philoscia* Latreille. Thomson (1893, p. 55, pl. 1, fig. 9) described and figured the inner lobe of the 1st maxilla in *O. punctatus* as ending in 5 teeth. I think he must have been mistaken here as it is usual in the Oniscoidea for this structure to bear setose processes instead. With this character excluded, Thomson's (1893) description itself might have been based on examples of any one of the four species of *Plymophiloscia* which I have collected in Tasmania. However, his specimens can be identified by the locality, as one of these species is common on Mt. Wellington while none of the other three has been found there at all.

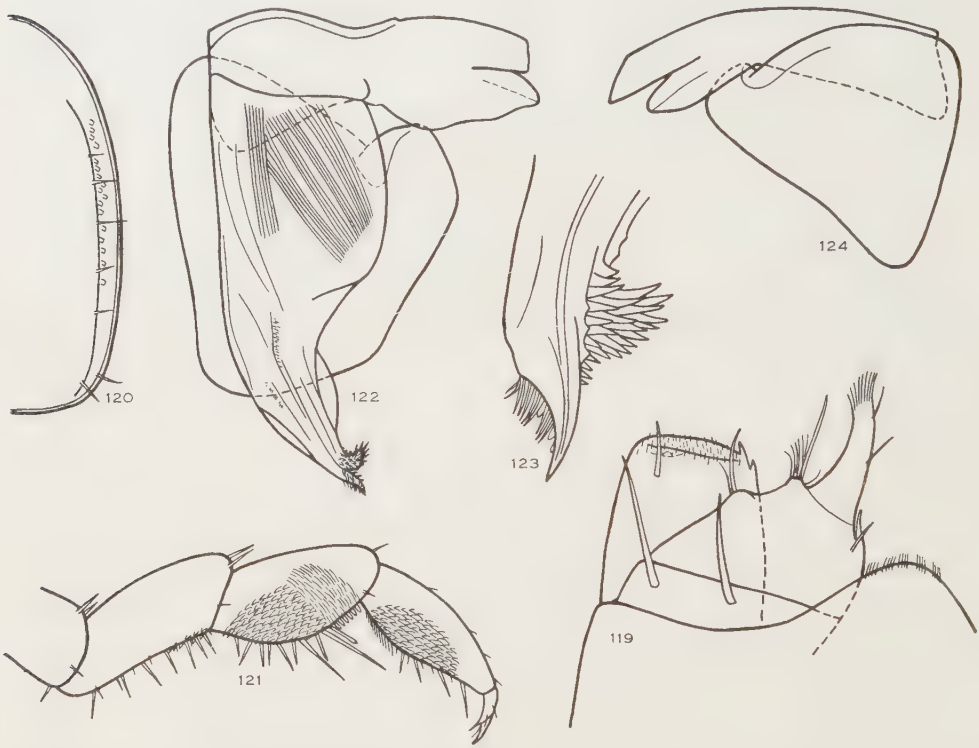
Budde-Lund (1908, p. 296) placed *O. punctatus* in a new genus, *Phalloniscus*. Scale-setae from *Ph. punctatus* (Thomson, 1879), as figured by Bowley (1935, figs. 23, 24), differ considerably from those exhibited by my specimens from Mt. Wellington. This confirms that the New Zealand and Tasmanian forms assigned to *O. punctatus* by Thomson are distinct.

As the name *Oniscus punctatus* Thomson, 1893 is a homonym of *Oniscus punctatus* Thomson, 1879, the specific name *punctatus* cannot be retained by the Tasmanian specimens. I therefore establish a new species, based on my specimens from Mt. Wellington, which replaces *O. punctatus* Thomson, 1893, and name this species *Plymophiloscia thomsoni* after the author of the latter.

Plymophiloscia tasmaniensis, sp. nov.

Figs. 119–124

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.



Figs. 119–124.—*Plymophiloscia tasmaniensis,* sp. nov.: *119,* distal part of left maxilliped, ventral view; *120,* right epimeron of 4th segment of pereion, dorsal view, showing gland pores; *121,* distal part of left 1st leg of male, anterior view; *122,* right 1st pleopod of male, dorsal view; *123,* distal part of endopodite of left 1st pleopod of male, ventral view; *124,* right 1st pleopod of female, ventral view.

Male

Size.—Length of largest specimen 6·3 mm, breadth 3·0 mm.

Colour.—As described for *Pl. thomsoni.*

Cephalon.—Eyes each composed of 19 ocelli. Otherwise as described for *Pl. thomsoni.*

First antenna.—As described for *Pl. thomsoni.*

Second antenna.—Length of peduncle 3·12 mm; length of articles of flagellum: 1st 0·32 mm, 2nd 0·27 mm, 3rd 0·43 mm. Spines and setae as for *Pl. thomsoni.*

Mandibles, 1st and 2nd maxillae.—As described for *Pl. thomsoni.*

Maxilliped (Fig. 119).—Distal set of setae on inner border of endopodite consists of 1 large seta and 6 or 7 smaller setae. Otherwise as described for *Pl. thomsoni.*

Pereion.—Shape of epimera and ornamentation of segments as described for *Pl. thomsoni.* Number of gland pores opening into each epimeral groove ranges from 13 to 23. Pores more numerous in anterior third, fewer in middle third, and absent from posterior third of groove. Epimeron of 4th segment illustrated in Figure 120.

Pereiopods.—As described for *Pl. thomsoni.* First leg illustrated in Figure 121.

Male organ.—As described for *Pl. thomsoni.*

Pleon.—Length (along mid-line) 1·60 mm; breadth (across 3rd segment) 1·65 mm. Otherwise as described for *Pl. thomsoni.*

First pleopod (Fig. 122).—Exopodite subquadrangular, outer border being bent outwards in a blunt curve; its apical angle bluntly rounded; its anterior border exhibits a fold near outer angle. Inner anterior angle of exopodite produced forwards to form a bluntly rounded lobe. Endopodite club-shaped with distal third bent outwards. Dorsal surface of endopodite exhibits irregular ridges, some ornamented with setae. There is a broad, oval, chitinous thickening on both inner and outer border of distal third. Apex of endopodite (Fig. 123) ends in a sharp curved point which is ridged on ventral surface, ornamented with conical processes on dorsal surface, and has a row of slender spines along its incurved inner margin. On outer side of dorsal surface, below base of curved apical point, is an outwardly directed protuberance completely covered with conical processes of varying lengths.

Second pleopod.—Exopodite subtriangular with outer border straight and apex sharply rounded. Setae and spines distributed as in *Pl. thomsoni.* Length of articles of endopodite: 1st 0·40 mm, 2nd 1·10 mm. Length of flagelliform portion of 2nd article 0·28 mm. Otherwise endopodite as described for *Pl. thomsoni.*

Third pleopod.—Exopodite subquadrangular with posterior border straight and apical angle sharply rounded.

Uropod.—Distance separating insertions of exopodite and endopodite 0·16 mm. Greatest length of protopodite 0·55 mm; length of rami: exopodite 0·88 mm, endopodite 0·51 mm. Otherwise as described for *Pl. thomsoni.*

Female

Length of largest specimen 7·8 mm, breadth 3·5 mm. Female differs from male in the following structures:

Pereiopods.—As described for *Pl. thomsoni.*

First pleopod (Fig. 124).—Exopodite subtriangular with outer border very slightly incurved and apex rather bluntly rounded; anterior border exhibits a fold near outer angle. Endopodite not developed.

Second and 3rd pleopods.—As described for *Pl. thomsoni.*

Habitat

Type locality.—Description is based on specimens found in debris on ledges of a cliff above the shore at Tinderbox, on 25.iii.1957; 24 males and 24 females obtained.

Other localities.—Specimens were found under stones on a damp hillside covered with dogwood, on Mt. Dromedary.

Variations

In some specimens from Tinderbox, the true brown pigmentation on dorsal surface is replaced by orange-brown on epimera, and over all of pleon except for the band of dark brown on each side. In other specimens, background colour of dorsal surface is completely orange-brown except for a broad band of dark brown down middle of body.

In one male specimen from Tinderbox, carpos and propodos of 1st and 2nd legs are broadened but there are no areas of large backwardly sloping scales on 1st–3rd legs.

Plymophiloscia notleyensis, sp. nov.

Figs. 125–131

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male

Size.—Length of largest specimen 7·1 mm, breadth 3·5 mm.

Colour.—In live animal, background colour of cephalon and pereion medium brown, background colour of pleon dark brown. The 3 dark bands on pereion and distribution of unpigmented markings as described for *Pl. thomsoni.*

Cephalon.—Eyes each composed of 19–21 ocelli. Otherwise as described for *Pl. thomsoni.*

First antenna.—As described for *Pl. thomsoni.*

Second antenna.—Length of peduncle 3·07 mm; length of articles of flagellum; 1st 0·38 mm, 2nd 0·30 mm, 3rd 0·49 mm. Spines and setae as described for *Pl. thomsoni.*

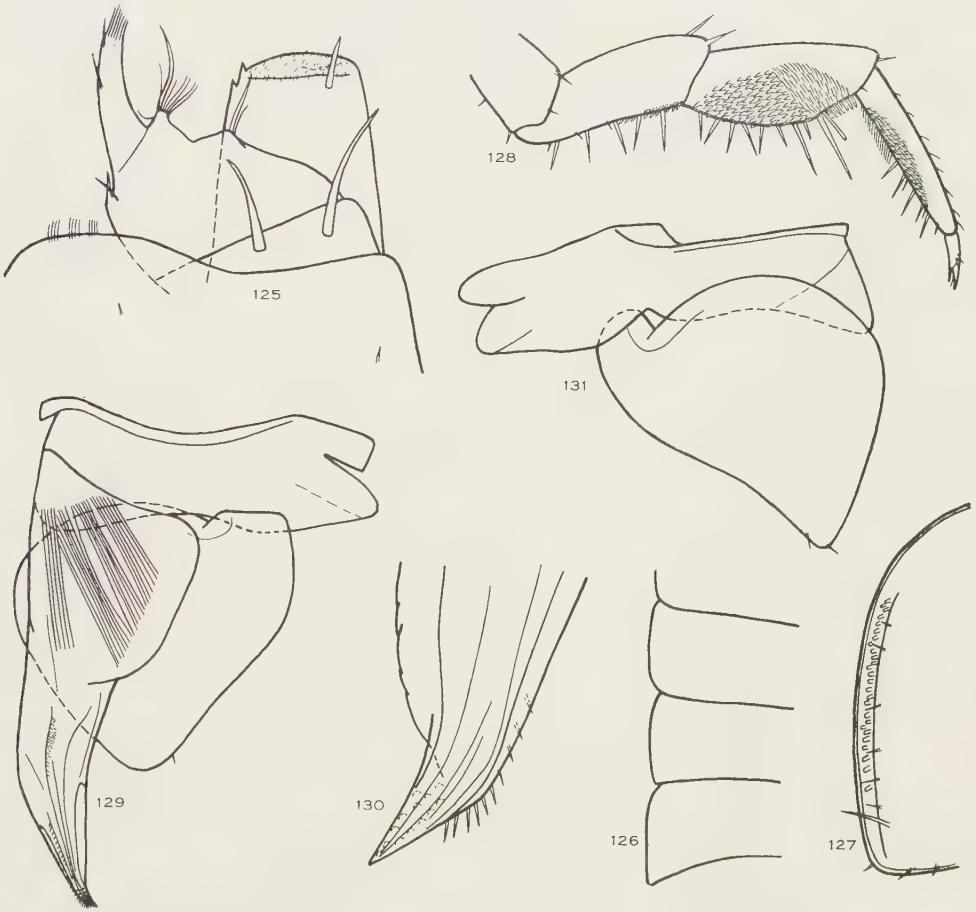
Mandibles.—Incisor process of left mandible consists of a bifid tooth and a smaller simple tooth. Otherwise mandibles as decribed for *Pl. thomsoni.*

First and 2nd maxillae.—As described for *Pl. thomsoni.*

Maxilliped (Fig. 125).—Distal set of setae on inner border of endopodite consists of one large seta and 6 or 7 smaller setae. Otherwise as described for *Pl. thomsoni.*

Pereion.—Posterior borders of 1st–3rd segments almost straight; their posterior angles bluntly rounded. Epimera of 4th segment very slightly produced backwards;

their posterior angles distinctly right-angled. Epimera of 3rd–5th segments shown in Figure 126. Shape of 5th–7th epimera as described for *Pl. thomsoni*. Number of gland pores opening into each epimeral groove ranges from 23 to 32. Pores more numerous in anterior half, fewer in third quarter, and absent from posterior quarter of groove. Epimeron of 4th segment shown in Figure 127. Ornamentation of segments as described for *Pl. thomsoni*.



Figs. 125–131.—*Plymophiloscia notleyensis*, sp. nov.: *125*, distal part of right maxilliped, ventral view; *126*, left epimera of 3rd–5th segments of pereion, dorsolateral view; *127*, left epimeron of 4th segment of pereion, dorsal view, showing gland pores; *128*, distal part of left 1st leg of male, anterior view; *129*, right 1st pleopod of male, dorsal view; *130*, distal part of endopodite of right 1st pleopod of male, ventral view (position of papillae on dorsal surface indicated by dots); *131*, right 1st pleopod of female, ventral view.

Pereiopods.—Carpos of 1st leg (Fig. 128) broadened dorsoventrally; its lower border curved outwards. Propodos not broadened; its upper and lower borders almost straight. Spines, setae, scales, and claws as described for *Pl. thomsoni*.

Carpos of 2nd leg only slightly broadened dorsoventrally. In 3rd–7th legs, carpos not broadened, hence its upper and lower borders not curved. Distribution of backwardly sloping scales on 2nd and 3rd legs as described for *Pl. thomsoni*.

Male organ.—As described for *Pl. thomsoni*.

Pleon.—Length (along mid-line) 1·70 mm, breadth (across 3rd segment) 1·80 mm. Otherwise as described for *Pl. thomsoni*.

First pleopod (Fig. 129).—Exopodite subtriangular with outer border very shallowly incurved and apex bluntly rounded; anterior border exhibits a fold near outer angle. Endopodite club-shaped, with distal third tapering and bent outwards. Dorsal surface of endopodite raised into ridges, some ornamented with scales or setae. There is a long, spindle-shaped, chitinous thickening on both inner and outer border of distal third. Apex of endopodite (Fig. 130) ends in a sharply pointed triangular lobe which is bent outwards at an angle to rest of distal third. Inner border of lobe is curved out and bears a row of spines. Ventral surface of lobe raised into ridges; its dorsal surface ornamented with papillate processes; no papillae visible in ventral view of endopodite.

Second pleopod.—Exopodite subtriangular with outer border slightly incurved and apical angle rather elongated posteriorly and sharply rounded. Setae and spines distributed as in *Pl. thomsoni*. Length of articles of endopodite: 1st 0·34 mm, 2nd 0·98 mm. Length of flagelliform portion of 2nd article 0·23 mm. Otherwise endopodite as described for *Pl. thomsoni*.

Third pleopod.—Exopodite subquadrangular with posterior border slightly incurved and apical angle sharply rounded.

Uropod.—Distance separating insertions of exopodite and endopodite 0·15 mm. Greatest length of protopodite 0·55 mm; length of rami: exopodite 1·02 mm, endopodite 0·54 mm. Otherwise as described for *Pl. thomsoni*.

Female

Length of largest specimen 10·0 mm, breadth 4·8 mm. Female differs from male in the following structures:

Pereiopods.—Carpos of 1st and 2nd legs not broadened dorsoventrally. No areas of backwardly sloping scales on 1st–3rd legs.

First pleopod (Fig. 131).—Exopodite subtriangular with outer border shallowly incurved, although curvature is more pronounced than in 1st exopodite of male, and apex sharply rounded; its anterior border exhibits a fold near outer angle. Endopodite not developed.

Second pleopod.—Exopodite subtriangular with outer border almost straight and apex more bluntly rounded than that of 2nd exopodite of male. Endopodite as described for *Pl. thomsoni*.

Third pleopod.—Posterior border of exopodite almost straight; apical angle more bluntly rounded than in 3rd exopodite of male.

Habitat

Type locality.—Description is based on specimens found under stones and among fallen leaves of eucalypt and dogwood, on a damp hillside at Notley Gorge; collections made were as follows: 26.v.1956, 4 males, 3 females; 26.xii.1956, 3 females; 16.vi.1957, 1 male, 5 females; 9.viii.1957, 42 males, 57 females.

Other localities.—Specimens were found among fallen leaves around the base of a eucalypt at Prospect Vale, near Launceston.

Variations

Intensity of pigmentation varies, so that in some specimens background colour of dorsal surface is almost uniformly dark. In some specimens the true brown coloration on dorsal surface is replaced by orange-brown on epimera, pleura, and terminal segment. In others background colour of dorsal surface is entirely orange-brown.

PLYMOPHILOSCIA ULVERSTONENSIS, sp. nov.

Figs. 132–139

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male

Size.—Length of largest specimen 6·6 mm, breadth 3·1 mm.

Colour.—Background colour of dorsal surface in live animal light brown. Dark bands on pereion and pleon and unpigmented areas as described for *Pl. thomsoni*.

Cephalon.—Eyes each composed of 19–22 ocelli. Otherwise as described for *Pl. thomsoni*.

First antenna.—As described for *Pl. thomsoni*.

Second antenna.—Length of peduncle 3·85 mm; length of articles of flagellum: 1st 0·55 mm, 2nd 0·40 mm, 3rd 0·53 mm. Spines and setae as for *Pl. thomsoni*.

Mandibles.—Incisor process of left mandible consists of a bifid tooth and 2 simple teeth. Otherwise mandibles as described for *Pl. thomsoni*.

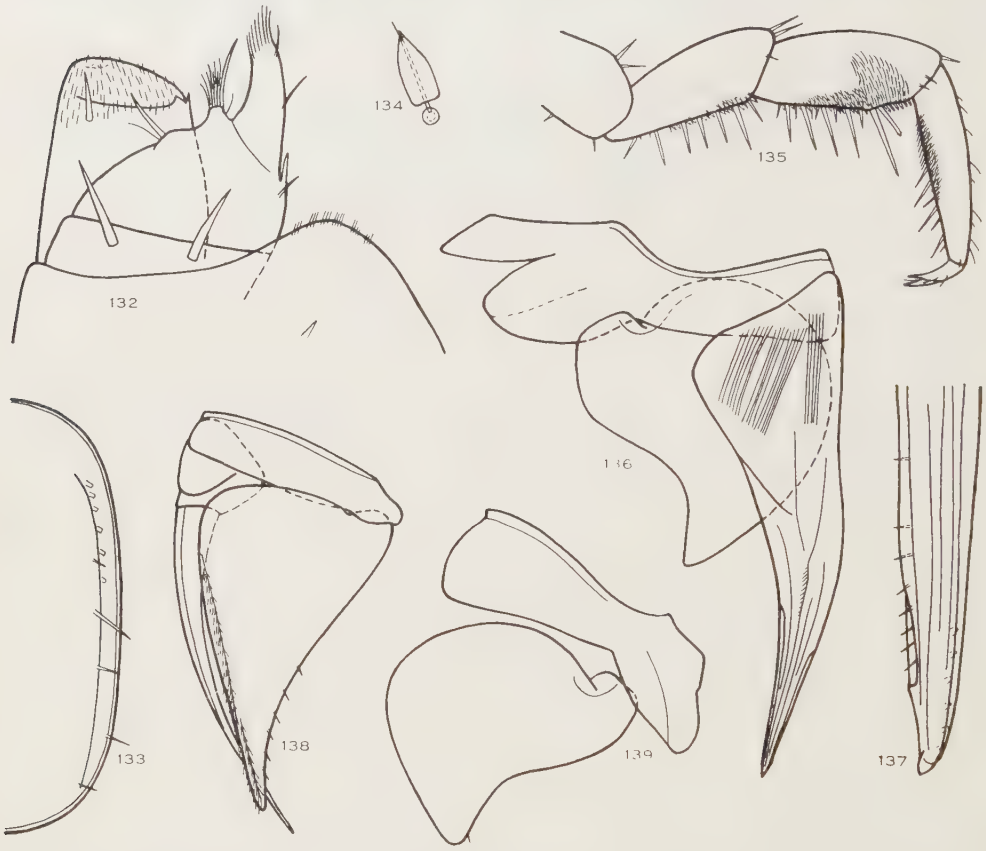
First and 2nd maxillae.—As described for *Pl. thomsoni*.

Maxilliped (Fig. 132).—Distal set of setae on inner border of endopodite consists of 1 large seta and 8–10 smaller setae. Apical region of endite bears moderately long scattered setae. Otherwise as described for *Pl. thomsoni*.

Pereion.—Shape of epimera as described for *Pl. thomsoni*. Dorsal surface smooth except for epimeral grooves. Number of gland pores opening into each groove ranges from 3 to 6. Pores occupy anterior third of groove and are absent from posterior two-thirds. Epimeron of 4th segment shown in Figure 133. Scales and spines on dorsal surface as described for *Pl. thomsoni*. Scale-setae occur on lower edge of lateral borders of segments; scale part of one of these scale-setae

(Fig. 134) subtriangular, not especially broad, with sides curved out and apex sharply pointed.

Pereiopods.—Carpos and propodos of 1st leg (Fig. 135) not broadened dorsoventrally, hence their upper and lower borders scarcely curved. Spine nearest distal end of carpos has its sheath divided into at least 8 points. Other spines,



Figs. 132–139.—*Plymophiloscia ulverstonensis,* sp. nov.: *132,* distal part of left maxilliped, ventral view; *133,* right epimeron of 4th segment of pereion, dorsal view, showing gland pores; *134,* scale-seta on lateral border of 1st segment of pereion, dorsal view; *135,* distal part of left 1st leg of male, anterior view; *136,* left 1st pleopod of male, dorsal view; *137,* distal part of endopodite of left 1st pleopod of male, ventral view (position of papillae on dorsal surface indicated by dots), *138,* left 2nd pleopod of male, ventral view; *139,* left 1st pleopod of female, ventral view.

spatulate scales, setae, and claws as described for *Pl. thomsoni.* Areas of projecting hyaline scales present on under surface of meros, under and anterior surfaces of carpos, and anterior surface of propodos; these spines slope slightly forwards towards distal end of article.

Carpos and propodos of 2nd and 3rd legs not broadened dorsoventrally. Areas of forwardly sloping hyaline scales occur on 2nd–4th legs.

Male organ.—As described for *Pl. thomsoni.*

Pleon.—Length (along mid-line) 1·60 mm, breadth (across 3rd segment) 1·65 mm. Apex of terminal segment forms an obtuse angle. Otherwise pleon as described for *Pl. thomsoni.*

First pleopod (Fig. 136).—Exopodite subtriangular with outer border deeply incurved and apex subacute; anterior border exhibits a fold near outer angle. Endopodite styliform and curved outwards, tapering evenly to a sharp apical point. Dorsal surface of endopodite raised into ridges; 1 ridge down centre ornamented with scales. With exception of a small, inwardly directed, chitinous point at its extreme tip, apical region (Fig. 137) not bent at an angle to rest of distal third. In an indentation in inner surface, a little above apical point, there is a row of spines. Ventral surface of apical region ridged; on dorsal surface near outer border is a row of papillate processes. No papillae visible in ventral view of endopodite.

Second pleopod (Fig. 138).—Exopodite subtriangular with outer border shallowly but distinctly incurved, and apex markedly elongated posteriorly and subacute. Setae and spines distributed as in *Pl. thomsoni.* Length of articles of endopodite: 1st 0·36 mm, 2nd 1·32 mm. Second article styliform; there is a chitinous thickening down outer edge of its basal two-thirds, beyond which article becomes very narrow and flagelliform. Length of flagelliform portion 0·43 mm.

Third pleopod.—Exopodite subquadrangular with posterior border shallowly but distinctly incurved and apical angle elongated posteriorly and sharply rounded.

Uropod.—Distance separating insertions of exopodite and endopodite 0·10 mm. Greatest length of protopodite 0·56 mm; length of rami: exopodite 1·00 mm, endopodite 0·53 mm. Otherwise as described for *Pl. thomsoni.*

Female

Length of largest specimen 7·6 mm, breadth 3·6 mm. Female differs from male in the following structures:

Pereiopods.—No areas of forwardly sloping hyaline scales on 1st–4th legs.

First pleopod (Fig. 139).—Exopodite subtriangular with outer border deeply incurved and apex sharply rounded; anterior border exhibits a fold near outer angle. Endopodite not developed.

Second pleopod.—Exopodite subtriangular with outer border slightly incurved and apex sharply rounded but not markedly elongated. Endopodite as described for *Pl. thomsoni.*

Third pleopod.—Posterior border of exopodite only slightly incurved; apical angle blunter and less elongated than in 3rd exopodite of male.

Habitat

Type locality.—Description is based on specimens found under stones and in debris on the ground immediately inland from a beach at West Ulverstone; collections made were as follows: 30.v.1956, 37 males, 59 females; 26.i.1958, 25 males, 53 females.

Other localities.—Specimens were found under trailing plants growing on a bank above the shore at Roaring Beach, South Arm.

Variations

Background colour of dorsal surface in some specimens is a moderately dark brown, but the 3 bands on pereion remain distinctly darker. In some specimens the true brown pigmentation of dorsal surface is replaced by orange-brown on epimera, pleura, and apical part of terminal segment.

IX. Family **PORCELLIONIDAE**

Genus PORCELLIO Latreille

Porcellio Latreille, 1804, p. 45.

Type species *Porcellio scaber* Latreille, 1804.

Generic Diagnosis

The following generic diagnosis is taken from Sars (1899, p. 176):

"Body oval, more or less depressed, with the lateral parts lamellarly expanded. Cephalon partly flanked by the side-plates of the 1st segment of mesosome, lateral lobes well developed, frontal lobe more or less projecting, and distinctly defined from the epistome. Metasome not abruptly contracted, epimeral plates of 3rd to 5th segments prominent and recurved; last segment conically produced. Eyes, as a rule, well developed, subdorsal. Antennae moderately slender, with the flagellum composed of 2 articulations only. Oral parts normal. Legs gradually increasing in length posteriorly, last pair in male sometimes differing from that in female. Opercular plates of the 2 anterior pairs of pleopoda, and sometimes also of the 3 succeeding pairs, provided with distinct air-cavities. Copulative organs of male of a similar structure to that in *Oniscus*. Uropoda distinctly projecting, outer ramus lanceolate, inner much smaller, linear, and originating far in front of the former."

Verhoeff (1917, p. 213) subsequently restricted *Porcellio* to species having pseudotracheae present only in the 1st and 2nd pleopods.

Porcellio scaber Latreille

Figs. 140, 141

Porcellio scaber Latreille, 1804, p. 45.
Porcellio graniger Miers, 1876, p. 226.
Further synonymy given by Budde-Lund (1885, p. 129).

Type specimens.—No longer in existence.

P. scaber is a cosmopolitan species which has evidently been introduced into Tasmania.

Distinguishing Characters

Length of largest male specimen 13·0 mm, breadth 6·0 mm; length of largest female specimen 12·5 mm, breadth 6·0 mm.

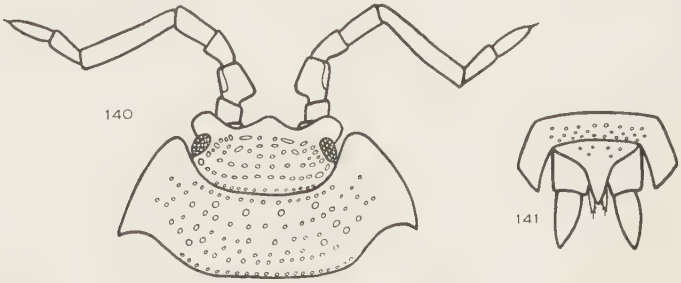
Live animal dark grey with lighter grey epimera and pleura. Animal not able to enrol.

Frontal line of cephalon (Fig. 140) produced into a subtriangular median lobe and subquadrangular lateral lobes. Vertex covered with large irregular

tubercles. Eyes compound. Length of articles of flagellum of 2nd antenna: 1st 0·63 mm, 2nd 0·67 mm.

Posterior borders of each of 1st–3rd epimera deeply incurved; those of 4th–7th epimera slope backwards in a shallow curve. Posterior angles of all segments of pereion subacute. Dorsal surface of pereion bears numerous large irregular tubercles.

Pleon not abruptly narrower than pereion. Pleura of 3rd segment subcrescentic; those of 4th and 5th segments subrectangular. Terminal segment (Fig. 141) subtriangular with lateral borders deeply incurved and apex subacute. All segments of pleon bear tubercles smaller than those on cephalon and pereion. Pseudotracheae present in exopodites of 1st and 2nd pleopods. Exopodite of uropod (Fig. 141) lanceolate, terminal in position on protopodite. Endopodite



Figs. 140 and 141.—*Porcellio scaber* Latreille: *140,* cephalon, 2nd antennae and 1st segment of pereion, dorsal view; *141,* fifth and terminal segments of pleon and uropods of male, dorsal view.

subcylindrical, inserted on inner side of protopodite near its base. In female, rami of uropod are shorter in relation to protopodite than in male. Lengths in a male specimen: protopodite (along inner border) 0·75 mm, exopodite 1·57 mm, endopodite 0·75 mm. Lengths in a female specimen: protopodite (along inner border) 0·71 mm, exopodite 1·00 mm, endopodite 0·68 mm.

Habitat

Description is based on specimens found in clumps of rushes growing above the shore at Dodge's Ferry, on 22.iii.1956; 33 males and 22 females obtained. Other examples were found among decaying vegetation and under objects lying on the ground at Cooee, Natone, Ulverstone, Sheffield, Sandy Beach (West Tamar), Launceston, Longford, Hobart, Collinsvale, Huonville, Dunalley, and Trial Harbour. Specimens were also collected from among debris lying a little above high tide level on the shore at Eaglehawk Neck, South Arm, Tinderbox, and Barnes Bay, Bruny I.

Variations

The following colorations of dorsal surface of live adult animals were noted: Grey except for orange epimera and pleura; completely orange; or mottled in dark and light brown, dark and light grey, or dark grey and orange.

Remarks

Haswell (1882, p. 280) included Tasmania in the distribution of *P. graniger*. Chilton (1901, pp. 139, 140) recognized *P. graniger* to be synonymous with *P. scaber* and stated that *P. scaber* had therefore been recorded from Tasmania.

X. Family **ARMADILLIDIIDAE**

Key to Genera of Armadillidiidae Represented in Tasmania

Eyes compound; posterior angle of 1st segment of pereion entire ....*Armadillidium*
Eyes simple; posterior angle of 1st segment of pereion cleft .....*Eluma*

Genus ARMADILLIDIUM Brandt

Armadillidium Brandt, 1833, p. 184.

Type species *Armadillo vulgaris* Latreille, 1804.

Generic Diagnosis

The following generic diagnosis is taken from Sars (1899, p. 188):

"Body oblong or elliptical in form, very convex, and capable of being rolled up into a perfect ball. Cephalon with the front distinctly marginate, lateral lobes rounded, and sharply defined at the base. Epistome vertical, forming above a triangular shield, advancing more or less beyond the frontal edge. Side-plates of 1st segment of mesosome large, securiform, not incised behind. Metasome semicircular, with the edges continuous throughout; last segment lamellar, quadrangular or triangular in form, not extending beyond the limits of the epimeral plates of the penultimate segment. Eyes distinct, lateral. Antennulae with the terminal joint but little produced. Antennae, as a rule, not attaining half the length of the body, penultimate peduncular joint scarcely longer than the 2nd; flagellum biarticulate. Opercular plates of only the first 2 pairs of pleopoda with air-cavities. Uropoda very short, with the basal part broad, lamellar, outer ramus spatulate, inner narrow, cylindric."

Edney (1953, p. 88), in defining *Armadillidium*, stated: "Eyes compound."

Armadillidium vulgare (Latreille)

Figs. 142, 143

Armadillo vulgaris Latreille, 1804, p. 48.
Armadillidium vulgare Milne-Edwards, 1840, p. 9.
Armadillidium subdentatum Haswell, 1882, p. 279.
Further synonymy given by Budde-Lund (1885, p. 67).

Type specimens.—No longer in existence.

A. vulgare is a cosmopolitan species which has evidently been introduced into Tasmania.

Distinguishing Characters

Length of largest male specimen 13·0 mm, breadth 6·0 mm; length of largest female specimen 15·0 mm, breadth 7·0 mm.

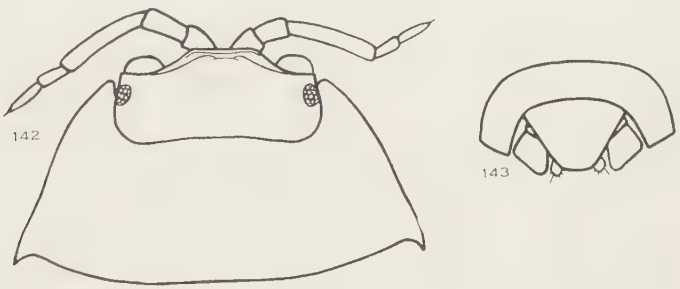
Live male specimen black; live female specimen mottled in dark and light brown. Animal able to enrol. Dorsal surface not setose.

Frontal line of cephalon (Fig. 142) produced into small right-angled lateral lobes. Antennary lobe on each side raised into a ridge visible in dorsal view of

cephalon. There is a raised triangular shield on frons; upper border of shield forms a ridge which projects beyond frontal line and curves back over it. Eyes compound. Length of articles of flagellum of 2nd antenna: 1st 0·56 mm, 2nd 0·76 mm.

Epimera of 1st segment of pereion (Fig. 142) produced backwards; their posterior angles subacute and entire, not cleft. Epimera of 2nd–5th segments trapezoidal with posterior angles bluntly rounded; those of 6th and 7th segments subrectangular with posterior angles right-angled.

Pleon semicircular; its lateral borders continuous with those of pereion. Pleura of 3rd–5th segments subrectangular and curved backwards. Terminal segment (Fig. 143) quadrangular, narrowing posteriorly, with lateral and posterior borders straight. Pseudotracheae present in exopodites of 1st and 2nd pleopods.



Figs. 142 and 143.—*Armadillidium vulgare* (Latreille): *142,* cephalon, 2nd antennae and 1st segment of pereion, dorsal view; *143,* fifth and terminal segments of pleon and uropods, dorsal view.

Exopodite of uropod (Fig. 143) occupies space between terminal segment and 5th pleuron. It is flattened and subquadrangular, terminal in position on protopodite. Endopodite subcylindrical, inserted on inner side of protopodite near its base.

Habitat

Description is based on specimens found in a garden rubbish heap in Hobart, on 9.iv.1956; 10 males and 5 females obtained. Other specimens were found in gardens in Launceston, under stones on Queen's Domain and in the University Park, Hobart, and in debris on ledges of a cliff above the shore at Tinderbox.

Remarks

Haswell (1882, p. 279) included Tasmania in the distribution of *A. subdentatum*. The only specimens of *Armadillidium* which I have found in Tasmania belong to *A. vulgare*, but their characters also agree with those described for *A. subdentatum* by Haswell. An examination of Haswell's specimens of *A. subdentatum* from Tasmania and Sydney, which are lodged in the Australian Museum, confirmed that this species is synonymous with *A. vulgare*.

Genus ELUMA Budde-Lund

Eluma Budde-Lund, 1879, p. 6, nomen nudum.
Eluma Budde-Lund, 1885, p. 47.

Type species *Eluma purpurascens* Budde-Lund, 1885.

Generic Diagnosis

The following generic diagnosis is taken from Collinge (1922, p. 103):

"Body oblong-ovate, strongly convex, setose, and closely and minutely punctured. Cephalon strongly marginate, with median and lateral lobes; epistome with sloping dorsal portion and keeled. Eyes simple, very small. Antennulae small, 3-jointed, terminal joint conical. Antennae somewhat short, flagellum bi-articulate. Pleural plates of mesosomatic segments 2–7 slightly excavate anteriorly, ventral margin indentate on segments 2–4, truncate on 6–7. Coxopodite of first segment separated from the pleuron and forming a notch on the posterior margin. Telson triangular, width greater than the length, not extending beyond the uropoda. Uropoda short, extending slightly beyond the telson; basipodite robust, thickened, antero-dorsal surface expanded, articulating ventro-anteriorly; exopodite flattened, expanded, laminate; endopodite styliform, elongated."

Figs. 144–146.—*Eluma caelatum* (Miers): *144*, cephalon, 2nd antennae and 1st segment of pereion, dorsal view; *145*, left epimeron of 1st segment of pereion, dorsolateral view; *146*, fifth and terminal segments of pleon and uropods, dorsal view.

ELUMA CAELATUM (Miers)

Figs. 144–146

Armadillidium caelatum Miers, 1877, p. 665, pl. 67, fig. 3.
Eluma purpurascens Budde-Lund, 1879, p 6, nomen nudum.
Eluma purpurascens Budde-Lund, 1885, p. 48
Eluma caelatum Collinge, 1917*a*, p. 115.

Location of Miers' type specimens.—British Museum (Natural History), London. Two males, one female. Register No. 79.21.

According to Collinge (1922, p. 105) the distribution of *E. caelatum* includes French Guiana, certain western European countries, Algeria, some Atlantic islands, and the Nicobar Is. As my specimens were found in or near populated areas it seems likely that the species has been introduced into Tasmania. I have seen no record of its occurrence elsewhere in the Australian region.

Distinguishing Characters

Length of largest male specimen 9·0 mm, breadth 4·0 mm; length of largest female specimen 10·5 mm, breadth 4·5 mm.

Live animal dark pinkish brown with lighter pink epimera and pleura. Animal able to enrol. Dorsal surface has dense covering of setae.

Frontal line of cephalon (Fig. 144) produced into small, right-angled, lateral lobes. Antennary lobe on each side raised into a ridge visible in dorsal view of cephalon. There is a raised triangular shield on frons; upper border of shield forms a ridge which meets frontal line. Eyes simple, each consisting of 1 large ocellus. Length of articles of flagellum of 2nd antenna: 1st 0·27 mm, 2nd 0·60 mm.

Epimera of 1st segment of pereion produced backwards; there is a low ridge down dorsal surface of 1st epimeron, near lateral border; posterior angle of epimeron cleft (Fig. 145). Epimera of 2nd–5th segments trapezoidal with posterior angles bluntly rounded; those of 6th and 7th segments subrectangular with posterior angles right-angled.

Pleon semicircular; its lateral borders continuous with those of pereion. Pleura of 3rd–5th segments subrectangular and curved backwards. Terminal segment (Fig. 146) subtriangular with lateral borders slightly curved outwards and apex sharply rounded. Pseudotracheae present in exopodites of 1st and 2nd pleopods. Exopodite of uropod (Fig. 146) occupies space between terminal segment and 5th pleuron. It is flattened and subquadrangular, terminal in position on protopodite. Endopodite subcylindrical, inserted on inner side of protopodite near its base.

Habitat

Description is based on specimens found under stones on Queen's Domain, Hobart, on 4.vi.1956 and 19.vii.1956; 12 males and 12 females obtained. Other specimens were found among decaying vegetation in gardens in Launceston and Hobart, under stones in the University Park, Hobart, and at Collinsvale, and in debris on ledges of a cliff above the shore at Tinderbox.

Remarks

Budde-Lund (1885, p. 49) himself suggested that *E. purpurascens* was perhaps not different from *Armadillidium caelatum*. This synonymy was confirmed by Collinge (1917*a*, 1922).

XI. Family **ARMADILLIDAE**

Key to Genera of Armadillidae Represented in Tasmania

Posterior angle of 1st segment of pereion entire, not cleft; lobe on under surface of 1st epimeron completely separated from epimeral border ..... *Cubaris*, s.s.

Posterior angle of 1st segment of pereion cleft; inner lobe, formed by cleft, continuous with lateral border of epimeron ..... *Sphaerillo*

Genus CUBARIS Brandt, s.s. after Verhoeff

Cubaris Brandt, 1833, p. 189.
Armadillo, section VI, Budde-Lund, 1904, p. 118.
Nesodillo Verhoeff, 1926, p. 275.
?*Spherillo*, section VIII, Budde-Lund, 1904, p. 66 (in part).

Type species *Cubaris murina* Brandt, 1833.

Budde-Lund (1904) grouped species of Armadillidae in two genera, *Spherillo* Dana, 1852, and *Armadillo* Brandt, 1833, at the same time altering the limits of both, and dividing *Spherillo* into 13 sections and *Armadillo* into seven sections. He referred to each of sections II, VI, and VII of *Armadillo* as *Cubaris* Brandt (in part), and (p. 97) designated "*Armadillo murinus* Br." (= *C. murina* Brandt, 1833) as the type species of section VI of *Armadillo*.

Verhoeff (1926, pp. 251, 259) considered that *Spherillo* and *Armadillo* could not be clearly separated on the characters which Budde-Lund (1904) used to distinguish them. In keys to genera of Armadillidae he (p. 252) restricted *Armadillo, Spherillo* (which he (p. 250) preferred to spell as *Sphaerillo*), and *Merulana* Budde-Lund, 1913, and established nine new genera, placing (p. 259) all of these genera except *Emydodillo* Verhoeff, 1926 in the group which he referred to as "*Armadillo* + *Sphaerillo* B.L.". He (p. 256) suggested that three of his new genera, *Nesodillo, Hawaiodillo,* and *Merulanella,* should possibly be grouped as subgenera of *Merulana* in the wider sense.

Verhoeff (p. 275) compared his new genus *Nesodillo* with Budde-Lund's sections of *Spherillo* and referred it to section VIII. He placed four of the species in this section in other new genera and judged the remainder, i.e. *Sph. speciosus* (Dana, 1853), *Sph. monolinus* Dana, 1853, *Sph. vitiensis* Dana, 1853, *Sph. aucklandicus* (Budde-Lund, 1885), and *Sph. tarangensis* Budde-Lund, 1904, as probably, but not definitely, belonging in *Nesodillo*. Verhoeff considered that of the species of *Spherillo* established by Wahrberg (1922), only *Sph. marmoratus* and *Sph. rufoniger* could possibly be included in *Nesodillo*. He assigned to *Nesodillo* nine species designated as new.

Herold (1931, p. 319) stated that *Cubaris murina* must be included in *Nesodillo,* and named it as *Nesodillo murinus*. Jackson (1933*a*, p. 90, 1933*b*, p. 157) identified *Nesodillo medius* Verhoeff, 1926 with *Cubaris murina,* and (1933*b*, p. 159) stated that *Nesodillo* must therefore be abandoned in favour of *Cubaris* Brandt (*C. murina* being the type species of *Cubaris*). Verhoeff (1938, p. 12) at first accepted Jackson's specific synonymy, although he incorrectly retained the generic name *Nesodillo,* and referred to *C. murina* as *N. murinus*. However, in a postscript to this same paper, he (p. 13) rejected the synonymy of the two species and retained *N. medius* as distinct from *N. murinus*. Jackson (1941, p. 3) stated that as *Nesodillo,* by Verhoeff's (1938) admission, contains *C. murina,* then *Nesodillo* and *Cubaris* are synonyms, and added that *Cubaris* has thus been clearly defined by both Brandt and Verhoeff and must be used only in this restricted sense. He (p. 16) reaffirmed the synonymy of *C. murina* and *C. medius*.

Vandel (1945, p. 254) referred to *Cubaris* as "*Cubaris s.str.* (= *Nesodillo* Verhoeff)", but added that *Merulana* Budde-Lund and *Merulanella* Verhoeff might perhaps be joined with this genus. I intend to follow Jackson (1941) in classing *Merulana* and *Merulanella,* and also *Hawaiodillo* Verhoeff, as genera distinct from *Cubaris,* s.s.

I propose the following diagnosis of *Cubaris*, s.s. (– *Nesodillo*) based on information of *Nesodillo* given by Verhoeff in his keys (pp. 252, 256, 263) and remarks on the genus (p. 275).

Generic Diagnosis

Frontal line of cephalon forms only a low ridge, neither drawn out into protuberances nor longitudinally furrowed in mid-line. Second antennae slenderly built with their greater part projecting out from cephalon. Dorsal surface of animal smooth, rugose, or tuberculate, but lacking spines. Posterior borders of 1st–6th segments of pereion more or less deeply incurved on each side, that of 7th segment straight or shallowly incurved on each side. Posterior angle of 1st epimeron entire, not cleft. If a small lobe is present on under surface of 1st epimeron it is not visible from outer side, and does not form a continuation of epimeral border. If a small lobe is present on under surface of 2nd epimeron it does not project beyond epimeral border. Pronotum occupies from one-fifth to one-quarter length of entire tergite. Terminal segment either constricted in the middle or not constricted; its dorsal surface not keeled; its posterior border bluntly rounded, straight or shallowly incurved, but not deeply incised in mid-line. Pleopods occupy considerably more than one-third breadth of pleon. Exopodites of all pleopods possess pseudotracheae. Breadth of protopodite of uropod, if greater than length of protopodite, is not more than 1·25 times the latter. Length of basal surface of protopodite not more than one-third length of entire protopodite. Inner border of protopodite incurved, but not angularly indented near insertion of exopodite. Outer side of protopodite not produced outwards to form a triangular lobe. Exopodite of uropod varies in length, but if very short (less than half breadth of lobe of protopodite), then free lobe of protopodite, measured on its inner border up as far as lateral indentation of terminal segment, is longer than it is broad across the middle. Exopodite inserted on dorsal surface of protopodite and distinctly removed from inner border of latter. Surface of protopodite not raised posterior to exopodite.

Where Verhoeff specified the terminal segment as not keeled, I interpret a keel as being a sharply defined ridge, such as he (1926, fig. 74) figured for *Merulanella wahrbergi* Verhoeff, 1926, and not a broad blunt elevation, extending down only a part of the length of the segment, such as occurs in the Tasmanian species which I assign to *Cubaris*, s.s.

I have automatically included in *Cubaris*, s.s. all species assigned to *Nesodillo* by Verhoeff (1926, 1928, 1936, 1938, 1942*b*, 1946), Jackson (1930, 1931), and Herold (1931). Verhoeff (1946) designated as new *N. burmanus*, *N. tenasserimus*, and *N. schellenbergi*, sub. sp. *malaisei*, but these were actually established in an earlier paper (1942*b*, pp. 169, 170). The species of *Spherillo* which Verhoeff (1926) suggested may belong in *Nesodillo* must also be considered here. Chilton (1910*b*, p. 290) listed *Sph. aucklandicus* as a synonym of *Sph. monolinus*. Information given in the original descriptions of *Sph. monolinus*, *Sph. speciosus*, and *Sph. tarangensis* is not sufficient to justify the transference of these species to *Cubaris*, s.s. *Sph. vitiensis*, according to Dana's (1853, p. 721) description, has a

rectangular notch in the inner border of the protopodite of the uropod, and is therefore excluded from *Cubaris*, s.s. I agree with Verhoeff that *Sph. marmoratus* and *Sph. rufoniger* may possibly be included in *Nesodillo* (and consequently in *Cubaris*, s.s.). Besides species originally placed in *Nesodillo* Jackson (1941, p. 16) included in *Cubaris*, s.s. the following: *C. galbineus* (Eschscholtz, 1823), *C. javanensis* (Dollfus, 1889), and *C. lifuensis* Stebbing, 1900.

I have collected examples of four species which I assign to *Cubaris*, s.s. These cannot be identified with species included in the restricted genus by previous authors, but before they can be regarded as new it is necessary also to compare them with any other established species assigned to *Cubaris*, s.l. which may remain in *Cubaris*, s.s. The number of species in *Cubaris*, s.l. is considerable, especially as some authors have used this name to replace *Armadillo*. I have seen no reference to any comprehensive attempt to determine which species of *Cubaris*, s.l. may be retained in *Cubaris*, s.s. Jackson's (1941) attempt covers only species found in Oceania. I have traced species of *Cubaris* by consulting Budde-Lund's (1904) revision and the Zoological Records for the years 1901–1956, and have then obtained further information on the species from revisions by Budde-Lund (1885, 1904), Barnard (1932), and Van Name (1936, 1942), and from the original descriptions of species not included in these works.

Budde-Lund (1904) referred to each of his sections II, VI, and VII of *Armadillo* as *Cubaris* Brandt (in part), but in a later paper (1909, p. 54), in which these sections were classed as subgenera of *Armadillo*, he named section II as *Diploexochus* Brandt and section VII as *Bethalus*, subgen. nov. He retained in subgenus *Cubaris*, of which *C. murina* is the type, only the species in his section VI and one other species, *A. emunitus* Budde-Lund, 1904, originally placed in section VII.

Chilton (1910*b*, p. 289) used the name *Cubaris* for the New Zealand species which Budde-Lund (1904) placed in *Spherillo*. Those belonging in section VIII have already been discussed. The remainder were included in other sections of *Spherillo* from which Verhoeff (1926, p. 275) dissociated *Nesodillo*.

Barnard (1932) excluded from *Bethalus* two species, *Armadillo tenuipunctatus* and *A. depressus* Dollfus, 1896, which were placed in section VII by Budde-Lund (1904).

Van Name (1936) extended *Cubaris* to completely replace *Armadillo*, s.l., and divided the species thus included in *Cubaris* into five groups. He assigned his groups I and II to subgenus *Venezillo* Verhoeff, 1928. *Venezillo* was later classed as a genus by Verhoeff (1933, p. 101). Van Name regarded the species in his group III as doubtful members of *Venezillo*. As these species all bear spines or spine-like tubercles on the dorsal surface they are in any case excluded from *Cubaris*, s.s. The species of *Cubaris* dealt with by Van Name (1942) in a supplement to his earlier work were placed in either his group I or his group II, and so may also be assigned to *Venezillo*. Other species which have been removed from *Cubaris* to other genera are shown in the following tabulation:

Species	Genus	Reference
C. dollfusi Stebbing, 1900	*Merulanella* Verhoeff, 1926	Verhoeff (1926, p. 357)
C. zebricolor Stebbing, 1900	*Sphaerillo* Verhoeff, 1926	Verhoeff (1926, p. 296)
C. warreni Collinge, 1917	*Bethalus* Budde-Lund, 1909	Barnard (1932, p. 315)
C. barnardi Collinge, 1920	*Bethalus* Budde-Lund, 1909	Barnard (1932, p. 317)
C. secutor Jackson, 1924	*Bethalus* Budde-Lund, 1909	Barnard (1932, p. 316)
C. ovampoensis Barnard, 1924	*Diploexochus* Brandt, 1833	Barnard (1932, p. 328)

A list of names of species of *Cubaris* which have been suppressed due to synonomy is given in Table 1.

TABLE 1

SPECIES OF CUBARIS SUPPRESSED DUE TO SYNONYMY

Species	Synonym of:	Reference
C. brunnea Brandt, 1833	*C. murina* Brandt, 1833	Richardson (1905, p. 645)
C. cubensis de Saussure, 1857	*C. murina* Brandt, 1833	Budde-Lund (1885, p. 28)
C. affinis Miers, 1877, non (Dana, 1854)	*C. murina* Brandt, 1833	Budde-Lund (1885, p. 28)
C. javanensis (Dollfus, 1889)	*C. murina* Brandt, 1833	Budde-Lund (1894, p. 603)
C. borellii (Dollfus, 1894)	*C. murina* Brandt, 1833	Van Name (1936, p. 387)
C. medius (Verhoeff, 1926)	*C. murina* Brandt, 1833	Jackson (1933*a*, 1933*b*, 1941)
C. akermani Collinge, 1920	*C. burnupi* Collinge, 1917	Barnard (1932, p. 377)
C. griseus Collinge, 1920	*C. burnupi* Collinge, 1917	Barnard (1932, p. 377)
C. kashmiri Jackson, 1935	*C. ignota* Arcangeli, 1934	Vandel (1945, p. 252)
C. officinalis Stebbing, 1900, non (Desmarest, 1825)	*Armadillo purpurascens* (Budde-Lund, 1912)	Jackson (1941, p. 15)
C. reticulatus Collinge, 1917	*Bethalus nigrinus* (Budde-Lund, 1885)	Barnard (1932, p. 308)
C. longicauda Collinge, 1917	*Bethalus nigrinus* (Budde-Lund, 1885)	Barnard (1932, p. 308)
C. trilobata Collinge, 1917	*Diploexochus flavescens* (Brandt, 1833)	Barnard (1932, p. 343)

Budde-Lund (1885, p. 28) listed *Armadillo conglobator* Budde-Lund, 1879 as a synonym of *C. murina* but later (1904, p. 125) described it as a distinct species. He (1904, p. 120) considered *C. cinerea* Brandt, 1833, *C. galbineus* (Eschscholtz, 1823), and *C. flavobrunneus* (Dollfus, 1896) to be close to, and possibly identical with, *C. murina*.

I have examined descriptions of the remaining species in *Cubaris*, s.l., and compared them with the generic characters of *Cubaris*, s.s.

None of the species in Budde-Lund's section VI of *Armadillo*, nor *A. emunitus*, can be excluded on any character from *Cubaris*, s.s. The other two

Tasmanian forms by means of a single key. For convenience they are therefore distinguished from other species in *Cubaris*, s.s., by means of the following key in which the first part deals with species assigned to *Cubaris*, s.s., or to *Nesodillo* by previous authors, the second part with species established by Budde-Lund, Dollfus, and Van Name, and the third part with species established by Collinge and Barnard. A subsequent key further differentiates the new Tasmanian forms.

Key to Species of the Genus Cubaris, s.s.

(a) Species Assigned by Previous Authors, and New Species

1. Posterior border of terminal segment incurved in the middle ..... *incisus, pronyensis, plasticus, burmanus*
   Posterior border of terminal segment straight or curved outwards 2
2. Terminal segment not constricted, its breadth being constant or decreasing posterior to its central incurvature 3
   Terminal segment constricted so that its breadth increases posterior to its central incurvature 5
3. Pereion lacking tubercles ..... *lifuensis, sarasini, longicornis, silvestris*
   Pereion tuberculate 4
4. Exopodite of uropod reaching posterior border of protopodite ..... *rufoniger*
   Exopodite of uropod not reaching posterior border of protopodite ..... *hickmani*, sp. nov.
5. Segments of pereion each with a transverse row of tubercles or swellings on each side of the mid-line ..... *murina, schellenbergi, fritschei*
   Segments of pereion without such an arrangement of tubercles or swellings 6*
6. Ventral surface of 1st epimeron with a ridge in front of lobe 7
   Ventral surface of 1st epimeron with no ridge in front of lobe 8
7. Length of 2nd article of flagellum of 2nd antenna less than twice length of 1st article ..... *canalensis, marmoratus*
   Length of 2nd article of flagellum of 2nd antenna three times length of 1st article ..... *tamarensis*, sp. nov.
8. Segments of pereion each with a transverse row of small pits in front of posterior border ..... *lacustris*
   Segments of pereion without small pits 9
9. Exopodite of uropod reaching posterior border of protopodite ..... *papuae*
   Exopodite of uropod not reaching posterior border of protopodite 10
10. Second epimeron with no lobe on its ventral surface ..... *pacificus*
    Second epimeron with a lobe on its ventral surface 11
11. Lobe on ventral surface of 2nd epimeron connected with epimeral border ..... *bocki*
    Lobe on ventral surface of 2nd epimeron not connected with epimeral border 12
12. Frontal line of cephalon not raised on a ridge ..... *verhoeffi*
    Frontal line raised on a ridge, at least at sides of cephalon 13
13. Frontal line depressed in the middle 14
    Frontal line not depressed in the middle 15
14. Segments of pereion smooth ..... *arcangelii, enoensis*
    Segments of pereion each with a low tubercle on each side above base of epimeron ..... *tasmaniensis*, sp. nov.

* I am uncertain of the position of *C. jonesii* here, as Verhoeff (1936, p. 102) stated that only indications of the swellings exhibited by *C. schellenbergi* are apparent in this species. I assign it to the second alternative in order to demonstrate its distinction from the Tasmanian species on other characters.

15. Endopodite of uropod narrowing distally with its apex sharply rounded .... *jonesii, tenasserimus*
Endopodite of uropod broadening distally with its apex bluntly rounded .... *sulcifrons,* sp. nov.

(*b*) *Species established by Budde-Lund, Dollfus, and Van Name, and New Species*

1. Second epimeron with no lobe on its ventral surface ....*egens, tenuipunctatus, depressus*
Second epimeron with a lobe on its ventral surface 2
2. Ventral surface of 1st epimeron with a ridge in front of lobe 3
Ventral surface of 1st epimeron with no ridge in front of lobe 5
3. Lobe on 1st epimeron with its apex acute .....*miser, proximatus, intermixtus*
Lobe on 1st epimeron with its apex blunt 4
4. Lateral processes of clypeus oval; eye composed of 22 or more ocelli .... *immotus, conglobator*
Lateral processes of clypeus subtriangular; eye composed of 15 ocelli .... *tamarensis,* sp. nov.
5. Exopodite of uropod reaching, or almost reaching, posterior border of protopodite .... *collinus, nigromarginatus*
Exopodite of uropod terminating distinctly in front of posterior border of protopodite ..6
6. Pereion with a series of prominent tubercles extending across each segment 7
Pereion without such a series of prominent tubercles 8
7. Second to 7th segments of pereion with 2 tubercles on each epimeron .....*cinchonae*
Second to 7th segments of pereion with one tubercle on each epimeron .... *hickmani,* sp. nov.
8. Second epimeron deeply cleft almost into 2 parts .....*glomerulus, albipes*
Second epimeron not deeply cleft, only with a small lobe on its ventral surface 9
9. Length of 2nd article of flagellum of 2nd antenna twice length of 1st article ..*emunitus*
Length of 2nd article of flagellum of 2nd antenna 2·5 times or more than 2·5 times length of 1st article 10
10. Segments of pereion each with a low tubercle on each side above base of epimeron .... *tasmaniensis,* sp. nov.
Segments of pereion without such tubercles 11
11. Frontal line of cephalon depressed in the middle .....*arcuatus*
Frontal line not depressed in the middle .....*sulcifrons,* sp. nov.

(*c*) *Species established by Collinge and Barnard, and New Species*

1. Posterior border of terminal segment incurved in the middle .....*annandalei*
Posterior border of terminal segment straight or curved outwards 2
2. Exopodite of uropod reaching posterior border of protopodite .... *caeruleus, dilectum, cavernosus*
Exopodite of uropod not reaching posterior border of protopodite 3
3. Length of 2nd article of flagellum of 2nd antenna twice or less than twice length of 1st article .....*solidulus, nacrum, gravelii, expansus, pusillus*
Length of 2nd article of flagellum of 2nd antenna 2·5 times or more than 2·5 times length of 1st article 4
4. Terminal segment not constricted, its breadth being constant posterior to its central incurvature .....*hickmani,* sp. nov.
Terminal segment constricted so that its breadth increases posterior to its central incurvature 5

5. Segments of pereion each with several tubercles on each side of the mid-line ..... *robusta, fragilis*
   Segments of pereion without such an arrangement of tubercles 6
6. Ventral surface of 1st epimeron with a ridge in front of lobe 7
   Ventral surface of 1st epimeron with no ridge in front of lobe 8
7. Dorsal surface of body granulate ..... *granulatus, burnupi, pongolae*
   Dorsal surface of body not granulate ..... *tamarensis*, sp. nov.
8. Endopodite of uropod narrowing distally with its apex sharply rounded ..... *brunneocaudatus, chiltoni, lobatus*
   Endopodite of uropod broadening distally with its apex bluntly rounded ..... *tasmaniensis*, sp. nov., *sulcifrons*, sp. nov.

Key to Species of Cubaris, s.s. Represented in Tasmania

1. Ventral surface of 1st epimeron with a ridge in front of lobe ..... *tamarensis*, sp. nov.
   Ventral surface of 1st epimeron with no ridge in front of lobe 2
2. Pereion with a row of prominent tubercles across each segment; breadth of terminal segment constant posterior to its central incurvature ..... *hickmani*, sp. nov.
   Pereion with segments smooth except for a low tubercle or slight rugosity, or both of these, on each side above epimera; breadth of terminal segment increasing again posterior to its central incurvature 3
3. Frons of cephalon with a deep, transverse groove below and parallel to frontal line; lateral processes of clypeus (in adult) produced upwards to form acute triangular lobes ..... *sulcifrons*, sp. nov.
   Frons of cephalon with no deep transverse groove; lateral processes of clypeus almost right-angled and scarcely produced upwards ..... *tasmaniensis*, sp. nov.

Cubaris hickmani, sp. nov.

Figs. 147–161

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male (Fig. 147)

Size.—Length of largest specimen 6·0 mm, breadth 2·9 mm.

Colour.—Dorsal surface of live animal mottled with dark brown, orange-brown, and yellow.

Cephalon (Fig. 148).—Centre of vertex crossed by 2 transverse ridges; there is a curved ridge to inner side of each eye, and behind this ridge on each side is an oval tubercle. Frontal line forms an uninterrupted ridge curved backwards towards vertex. Frons shallowly depressed on each side to receive 2nd antennae; no deep groove above these depressions. Lateral processes of clypeus appear right-angled in anterior view and are scarcely produced upwards. Eyes rounded, each composed of 11–13 ocelli.

First antenna.—Triarticulate; 3rd article has a group of setae near apex.

Second antenna.—Length of peduncle 1·95 mm; length of articles of flagellum: 1st 0·10 mm, 2nd 0·41 mm. All articles of antenna bear spiny setae. Second article of flagellum ends in a process formed of partly fused setae.

Figs. 147–161.—*Cubaris hickmani,* sp. nov.: *147,* male specimen, dorsal view (cephalon and pleon foreshortened due to curvature of animal); *148,* cephalon, anterior view (antennae and mouthparts removed); *149,* distal part of left mandible, dorsal view; *150,* distal part of right mandible, dorsal view; *151,* distal part of outer lobe of right 1st maxilla, ventral view; *152,* distal part of inner lobe of right 1st maxilla, ventral view; *153,* distal part of left maxilliped, ventral view; *154,* right epimera of 1st and 2nd segments of pereion, ventrolateral view; *155,* scale-seta on dorsal surface of 1st segment of pereion, dorsal view; *156,* terminal segment and uropods, dorsal view; *157,* left 1st pleopod of male, dorsal view; *158,* left 2nd pleopod of male, ventral view; *159,* right uropod, dorsal view; *160,* left 1st pleopod of female, ventral view; *161,* right 2nd pleopod of female, ventral view.

Left mandible (Fig. 149).—Incisor process ends in 3 teeth, central tooth being weakly bifid and lateral teeth simple. Lacinia mobilis ends in 2 teeth. Setose lobe bears 2 pencils of setae; 1 pencil behind lobe. Molar portion represented by a tuft of plumose setae set on a common basal process.

Right mandible (Fig. 150).—Incisor process consists of 1 bifid tooth and 1 simple tooth. Lacinia mobilis irregular in shape. Setose lobe bears 1 pencil of setae; 1 pencil behind lobe. Molar portion like that of left mandible.

First maxilla.—Outer lobe (Fig. 151) bears 10 simple teeth, forming an outer group of 4 large teeth and an inner group of 6 more slender teeth. On ventral surface is a short spine below base of 4th large tooth. Inner lobe (Fig. 152) bears 2 short, thick, blunt setose processes.

Second maxilla.—Apex divided into 2 subrectangular lobes. Distal region of inner lobe densely setose; that of outer lobe has sparser covering of setae. Two coarse setae project into notch between lobes.

Maxilliped (Fig. 153).—Ischion distinct; 2 long spines on its ventral surface. Division of remainder of endopodite into 2 articles indicated by a faint oblique suture line across ventral surface. There are 2 sets of setae on inner border of 1st of these articles; basal set consists of 1 large and 1 smaller seta, distal set of 1 large seta and 3 smaller setae. Three setae occur singly on outer border of endopodite; near lowest one is a pencil which itself lacks setae. Endopodite ends in a tuft of setae. Endite subquadrangular in outline, its apex shallowly indented. It has 2 large spines to ventral side of indentation, a small spine on each side of apex, and a few spinules on outer border.

Pereion.—First epimera sharply rounded anteriorly. Outer side of 1st epimeron revolute, so that dorsal surface of epimeron is concave; its lateral margin simple, lacking a marginal furrow. Posterior angle of 1st epimeron sharply rounded and not cleft. On ventral surface of epimeron is a small rounded lobe which has no connection with lateral margin (see Fig. 154). Surface anterior to lobe not grooved or ridged. Posterior angle of 2nd epimeron rounded and not cleft. On ventral surface of 2nd epimeron is a small bluntly rounded lobe, situated well in front of posterior angle and not connected with epimeral margin (see Fig. 154). Ventral surface of 3rd epimeron slightly thickened near its anterior border. Epimera of 3rd and 4th segments trapezoidal and rounded posteriorly, those of 5th–7th segments quadrangular with posterior angles subacute. Epimera of all segments directed backwards. Between epimera, posterior border of tergite is almost straight in 1st–4th segments; in 5th and 6th segments it is produced into a median point; in 7th segment it has a large median point with a smaller point on each side of it. Ratio of length of pronotum to length of entire tergite (measured in the mid-line) 1 : 4·4 in 2nd segment and approximately 1 : 4·0 in 3rd–7th segments. Lengths in 2nd segment: pronotum 0·20 mm, entire tergite 0·88 mm; lengths in 3rd segment: pronotum 0·24 mm, entire tergite 0·94 mm. Dorsal surface tuberculate. Four pairs of large tubercles on each segment together form 8 longitudinal rows down pereion. On 1st segment there is a median eminence in front of central pair of tubercles. On each side of pereion there is a small rounded

tubercle to inner side of 2nd large tubercle on all segments, and 2 narrow tubercles occur between 2nd and 3rd large tubercles on 1st–6th segments, with 1 such tubercle in this position on 7th segment. Tubercles forming outermost pair not very pronounced on 4th segment; on 6th and 7th segments they project beyond posterior border of tergite. Tergites have covering of rounded scales and also bear numerous scale-setae. Scale-seta (Fig. 155) has a broad, V-shaped scale portion, with apex produced to form a narrow fold into which a short seta projects.

Pereiopods.—Each of large spines on under surface of 1st leg has its apex divided into several points. Spines on under surface of meros and carpos too sparse to appear as a brush. Leg also bears simple spiny setae. Dactylos has terminal claw and accessory claw. A long simple seta is in angle between claws.

Male organ.—Conical in outline. Its 2 ducts remain distinct and open separately under a flap on its dorsal surface.

Pleon.—Outline of pleon semicircular, continuous with that of pereion. Pleura of 3rd–5th segments expanded laterally, and curved backwards, subrectangular in shape, with 4th and 5th pairs each narrower and more rounded than preceding pair. Posterior border of each of 1st–4th tergites forms a blunt median angle which is progressively more obtuse in each succeeding segment; middle of posterior border of 5th tergite nearly straight. No tubercles present on 1st–5th segments. No lobes on ventral surface of 3rd–5th pleura. Terminal segment (Fig. 156) curves inwards on both sides at about middle of its length. Posterior half of segment subquadrangular with posterior border straight; its breadth is constant at 0·49 mm, not increasing posteriorly. There is a pair of oval tubercles on dorsal surface in centre of basal half of segment; surface behind tubercles is raised into a broad, median, longitudinal ridge, which does not extend to posterior border. Tergites bear scales and scale-setae similar to those on pereion.

First pleopod (Fig. 157).—Exopodite pear-shaped; outer tracheal part smaller than inner laminar part; spines on ventral surface near posterior border of laminar part. Endopodite styliform, its distal half curved outwards with a narrow chitinous thickening down outer edge. On dorsal surface a ridge, ornamented with small scales, extends down centre of distal part of endopodite. Surface to inner side of ridge indented, forming a shallow groove. A row of spinules occurs between ridge and inner border of endopodite.

Second pleopod (Fig. 158).—Exopodite subtriangular with outer border incurved and apical region greatly elongated. Tracheal part occupies outer lobe of exopodite. On ventral surface, spines are present near outer border of laminar part, and an area covered with fine setae extends forwards for some distance from apex. Length of articles of endopodite: 1st 0·22 mm, 2nd 0·95 mm. First article quadrangular in outline. Second article styliform; it has a chitinous thickening down outer edge of its basal five-eighths, beyond which article becomes very narrow and flagelliform. Length of flagelliform portion 0·37 mm.

Third pleopod.—Exopodite subtriangular with outer border incurved; its apical region elongated but to a lesser degree than that of 2nd exopodite. Tracheal

part occupies outer lobe of exopodite. There are spines on ventral surface near outer border of laminar part, and comb-setae on inner border. On dorsal surface, a short scale-covered ridge extends backwards from inner anterior angle.

Uropod (Figs. 156, 159).—Basal surface of protopodite oblique, visible in dorsal view of uropod; it occupies approximately one-third length of entire protopodite; its breadth less than length of protopodite. Length of basal surface 0·22 mm; breadth of basal surface 0·47 mm; length of entire protopodite 0·62 mm. Beyond basal surface, inner border of protopodite deeply and evenly incurved so that free lobe of protopodite becomes suddenly narrower posteriorly; its posterior margin obliquely rounded. Greatest length of lobe 0·50 mm; length of posterior margin 0·14 mm. Area of protopodite visible to outer side of terminal segment, when uropod is attached, longer on its inner side than it is broad; length (along inner edge as far as indentation of terminal segment) 0·30 mm; breadth (in a line across insertion of exopodite) 0·22 mm. Exopodite subcylindrical and inserted on dorsal surface of lobe, a little removed from its inner border; it does not reach to posterior border of protopodite. Above base of exopodite, protopodite is raised into a subtriangular prominence, inner angle of which overlaps inner margin of lobe. Endopodite inserted on ventral surface, near inner border, at base of protopodite. It is subcylindrical, narrowing distally, with apex sharply rounded. It does not reach to posterior border of terminal segment. Length of rami: exopodite 0·12 mm, endopodite 0·32 mm.

Female

Length of largest specimen 6·0 mm; breadth 3·0 mm. Female differs from male in the following structures:

First pleopod (Fig. 160).—Exopodite suboval, very short and broad; inner laminar part and outer tracheal part subequal in area. Endopodite not developed.

Second pleopod (Fig. 161).—Exopodite subtriangular, very short and broad, with outer border incurved and apex sharply rounded but not markedly elongated. Tracheal part occupies outer angle. Endopodite not developed.

Third pleopod.—Exopodite similar in shape to that of 2nd pleopod of female; no scaly ridge on its dorsal surface.

Habitat

Type locality.– Description is based on specimens found in debris and under logs in a forest of eucalypts and tree ferns at Tarraleah, on 7.x.1957; 51 males and 29 females obtained. Specimens were previously collected from this locality by Professor Hickman in January 1954 and January 1957.

Other localities.—Specimens were found under a eucalypt log at Wayatinah.

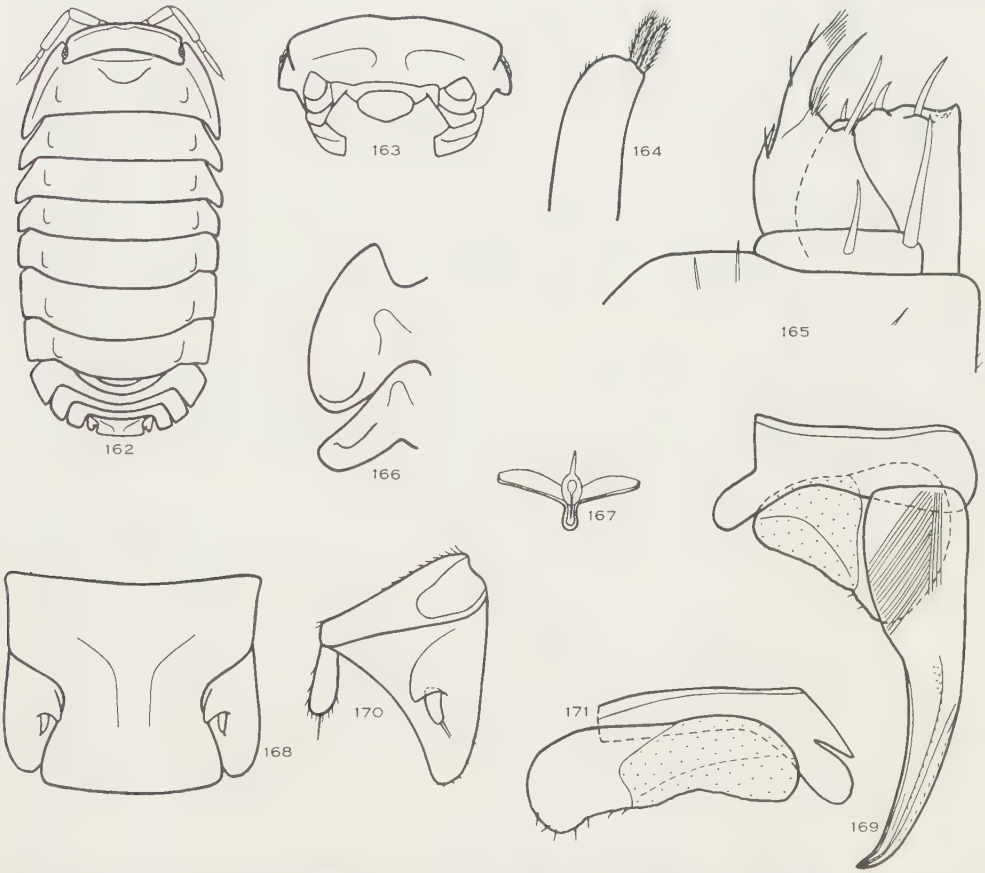
Remarks

This species is named after Professor V. V. Hickman who presented me with the examples from his collection and thereby drew my attention to the species.

Cubaris tasmaniensis, sp. nov.

Figs. 162–171

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.



Figs. 162–171.—*Cubaris tasmaniensis*, sp. nov.: *162*, male specimen, dorsal view (cephalon and pleon foreshortened due to curvature of animal); *163*, cephalon, anterior view (antennae and mouthparts removed); *164*, distal part of inner lobe of right 1st maxilla, ventral view; *165*, distal part of right maxilliped, ventral view; *166*, right epimera of 1st and 2nd segments of pereion, ventrolateral view; *167*, scale-seta on dorsal surface of 1st segment of pereion, dorsal view; *168*, terminal segment and uropods, dorsal view; *169*, left 1st pleopod of male, dorsal view; *170*, right uropod, dorsal view; *171*, left 1st pleopod of female, ventral view.

Male (Fig. 162)

Size.—Length of largest specimen 6·3 mm, breadth 3·1 mm.

Colour.—Background colour of dorsal surface in live animal purplish brown. Cephalon and pereion exhibit unpigmented patches. Protopodites of uropods orange.

Cephalon (Fig. 163).—Surface of vertex smooth except for a pair of very low tubercles immediately behind frontal ridge. Frontal line forms a ridge which is curved backwards towards vertex and shallowly depressed in mid-line. Frons has no transverse groove below frontal ridge; it is indented by 2 shallow depressions for 2nd antennae. Lateral processes of clypeus appear right-angled in anterior view and are scarcely produced upwards. Eyes rounded, each composed of 12–14 ocelli.

First antenna.—As described for *C. hickmani.*

Second antenna.—Length of peduncle 2·15 mm; length of articles of flagellum: 1st 0·15 mm, 2nd 0·45 mm. Setae as described for *C. hickmani.*

Mandibles.—Incisor process of left mandible consists of 1 strongly bifid tooth and 1 simple tooth. Otherwise mandibles as described for *C. hickmani.*

First maxilla.—Outer lobe as decribed for *C. hickmani.* Inner lobe (Fig. 164) bears 2 moderately long, blunt, setose processes.

Second maxilla.—No coarse setae between lobes. Otherwise as described for *C. hickmani.*

Maxilliped (Fig. 165).—Distal set of setae on inner border of endopodite consists of 1 large seta and 4 smaller setae. Otherwise endopodite as described for *C. hickmani.* Endite subquadrangular. Its apical region is uneven and bears 3 spines which decrease in size from innermost one outwards. At inner angle is a small depression in which is a short blunt spine.

Pereion.—First epimera subacute anteriorly. Outer side of 1st epimeron revolute, so that dorsal surface of epimeron is concave. Its lateral margin simple, lacking a marginal furrow; its posterior angle sharply rounded and not cleft. On ventral surface of 1st epimeron is a broad, bluntly rounded lobe which is not connected with lateral margin (see Fig. 166). Surface anterior to lobe not grooved or ridged. Posterior angle of 2nd epimeron rounded and not cleft. On ventral surface of 2nd epimeron is an elongated blunt lobe, situated well in front of posterior angle and not connected with epimeral margin (see Fig. 166). Ventral surface of 3rd epimeron slightly thickened near its anterior margin. Epimera of 3rd and 4th segments trapezoidal and rounded posteriorly; those of 5th–7th segments quadrangular with posterior angles almost right-angled. Epimera of all segments directed backwards. Between epimera, posterior borders of all tergites run straight. Ratio of length of pronotum to length of entire tergite (measured in the mid-line) 1 : 5·4 in 2nd segment and approximately 1 : 4·5 in 3rd–7th segments. Lengths in 2nd segment: pronotum 0·20 mm, entire tergite 1·08 mm; lengths in 3rd segment: pronotum 0·25 mm, entire tergite 1·13 mm. There is a shallow, median, semicircular groove on 1st tergite. On all segments there is a very low oval tubercle on each side above bases of epimera; these tubercles together form a line down each side of pereion. There is a slightly rugose area to inner side of each tubercle; remainder of dorsal surface smooth. Tergites have covering of rounded scales and also bear scattered scale-setae. Scale-seta (Fig. 167) has a short broad scale portion produced posteriorly in centre to form a club-shaped fold into which a short seta projects.

Pereiopods.—First leg has numerous spines set close together to form a brush on under surface of meros and carpos; otherwise as described for *C. hickmani*. Spines on under surface of meros become progressively sparser on 2nd–7th legs.

Male organ.—As described for *C. hickmani*.

Pleon.—Outline of pleon semicircular, continuous with that of pereion. Pleura of 3rd–5th segments expanded laterally and curved backwards, subrectangular in shape with 4th and 5th pairs each narrower than preceding pair. First to 5th segments smooth dorsally; between pleura their posterior borders evenly curved. No lobes on ventral surface of 3rd–5th pleura. Terminal segment (Fig. 168) curves inwards on both sides at about middle of its length; beyond this narrowing its breadth increases again considerably. Breadth across central constriction 0·52 mm; maximum breadth of posterior part 0·68 mm. Posterior border of segment almost straight. Dorsal surface of terminal segment raised into a broad, median, longitudinal ridge, which does not extend to posterior border. Tergites of pleon bear scales and scale-setae similar to those on pereion.

First pleopod (Fig. 169).—Exopodite subtriangular with apex bluntly rounded, spines on its ventral surface near apex. Tracheal part occupies approximately outer half of exopodite. Endopodite styliform with distal half curved outwards; apical tip of latter still further curved outwards at a slight angle to the rest. There is a narrow chitinous thickening on outer edge of distal half. A ridge ornamented with small scales extends down centre of dorsal surface of distal half. Surface to inner side of ridge is indented, the shallow groove so formed being limited on inner side by another less prominent ridge. There is a row of spinules on dorsal surface near inner border.

Second pleopod.—Exopodite as described for *C. hickmani*. Length of articles of endopodite: 1st 0·28 mm, 2nd 1·23 mm. Length of flagelliform portion of 2nd article 0·46 mm. Otherwise endopodite as described for *C. hickmani*.

Third pleopod.—As described for *C. hickmani*.

Uropod (Figs. 168, 170).—Basal surface of protopodite oblique, visible in dorsal view of uropod; it occupies approximately one-third length of entire protopodite; its breadth less than length of protopodite. Length of basal surface 0·22 mm; breadth of basal surface 0·52 mm; length of entire protopodite 0·67 mm. Beyond basal surface, inner border of protopodite shallowly and obliquely incurved so that free lobe of protopodite gradually becomes considerably narrower posteriorly; its posterior margin obliquely rounded. Greatest length of lobe 0·55 mm; length of posterior margin 0·09 mm. Area of lobe visible to outer side of terminal segment, when uropod is attached, longer on its inner side than it is broad; length (along inner edge as far as indentation of terminal segment) 0·35 mm; breadth (in a line across insertion of exopodite) 0·22 mm. Exopodite subcylindrical and inserted on dorsal surface of protopodite, away from its inner border. Exopodite terminates considerably in front of posterior border of protopodite. Anterior to base of exopodite, surface of protopodite is raised into a subtriangular prominence. When uropod is attached, inner angle of prominence overlaps lateral border of terminal segment. Endopodite inserted on ventral

surface, near inner border, at base of protopodite. It is subcylindrical, broadening distally, with apex bluntly rounded. Endopodite terminates far in front of posterior border of terminal segment. Length of rami: exopodite 0·12 mm, endopodite 0·24 mm.

Female

Length of largest specimen 6·8 mm, breadth 3·4 mm. Female differs from male in the following structures:

Pereiopods.—Large spines on under surface of meros and carpos less numerous than on corresponding legs of male.

First pleopod (Fig. 171).—Exopodite subrectangular, very short and broad; inner laminar part almost as large as outer tracheal part. Endopodite not developed.

Second pleopod.—Exopodite as described for *C. hickmani*. A conical process, projecting back from inner side of protopodite, probably represents an endopodite.

Third pleopod.—As described for *C. hickmani*.

Habitat

Type locality.—Description is based on specimens found in debris on ledges of a cliff above the shore at Tinderbox, on 25.iii.1957, 27.v.1957, 4.viii.1957, and 19.xi.1957; a total of 11 males and 25 females was obtained.

Other localities.—Specimens were found under stones at East Risdon.

Variation

Protopodites of uropods of some specimens are coloured purplish brown like rest of dorsal surface.

Cubaris sulcifrons, sp. nov.

Figs. 172–180

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male

Size.—Length of largest specimen 9·0 mm, breadth 4·5 mm.

Colour.—Dorsal surface of live specimen greyish brown mottled with unpigmented patches. Protopodites of uropods orange.

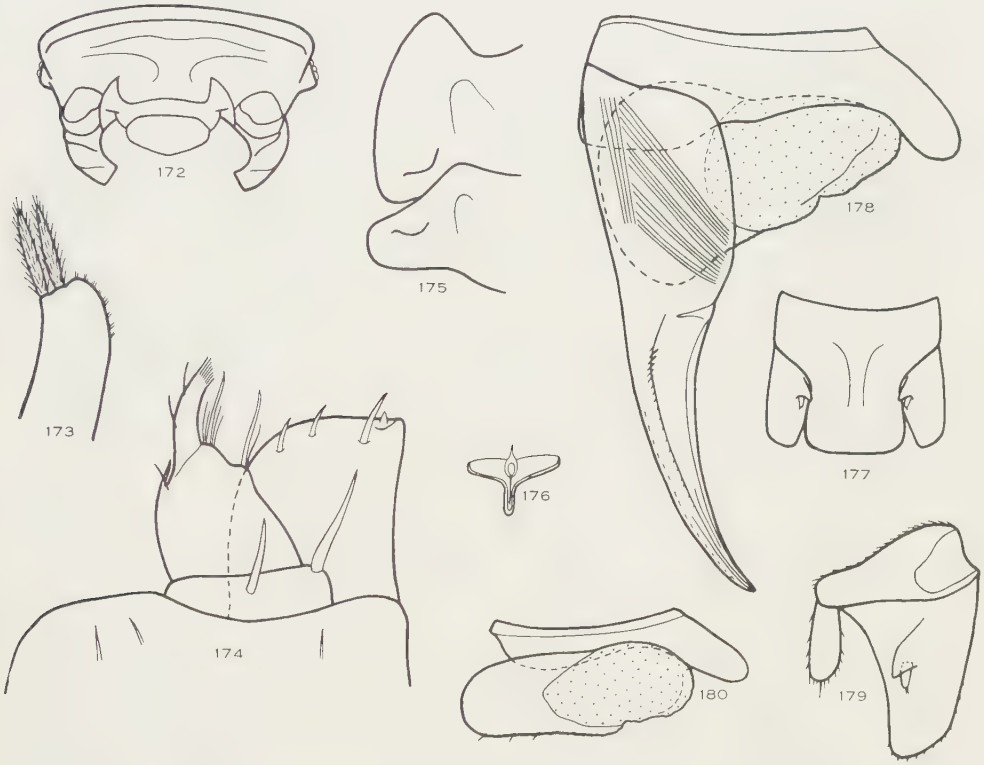
Cephalon (Fig. 172).—Surface of vertex smooth except for a pair of very low tubercles immediately behind frontal ridge. Frontal line forms an uninterrupted ridge, only slightly curved backwards. Frons indented by a deep groove running parallel to frontal ridge. Region of frons between this groove and depressions for 2nd antennae forms a subtriangular prominence. Lateral processes of clypeus produced upwards to form large, acute, triangular lobes. Eyes rounded, each composed of 12–14 ocelli.

First antenna.—As described for *C. hickmani*.

Second antenna.—Length of peduncle 2·92 mm; length of articles of flagellum: 1st 0·21 mm, 2nd 0·53 mm. Setae as described for *C. hickmani.*

Mandibles.—Incisor process of left mandible consists of 3 simple teeth, the central tooth being larger than others. Otherwise mandibles as described for *C. hickmani.*

First maxilla.—Outer lobe as described for *C. hickmani.* Inner lobe (Fig. 173) bears 2 moderately long, sharply pointed, setose processes.



Figs. 172–180.—*Cubaris sulcifrons,* sp. nov.: *172,* cephalon, anterior view (antennae and mouthparts removed); *173,* distal part of inner lobe of left 1st maxilla, ventral view; *174,* distal part of right maxilliped, ventral view; *175,* right epimera of 1st and 2nd segments of pereion, ventrolateral view; *176,* scale-seta on dorsal surface of 1st segment of pereion, dorsal view; *177,* terminal segment and uropods, dorsal view; *178,* right 1st pleopod of male, dorsal view; *179,* right uropod, dorsal view; *180,* left 1st pleopod of female, ventral view.

Second maxilla.—On dorsal surface at base of inner lobe is a V-shaped band of chitin. Otherwise as described for *C. hickmani.*

Maxilliped (Fig. 174).—Distal set of setae on inner border of endopodite consists of 1 large seta and 4 smaller setae. Otherwise endopodite as described for *C. hickmani.* Endite subquadrangular with outer apical angle rounded. There are 3 spines on its ventral surface near apex, innermost one being larger than others. Inner angle of apex exhibits a small indentation in which is a short blunt spine.

Pereion.—First epimera sharply rounded anteriorly. Outer side of 1st epimeron revolute, making dorsal surface of epimeron concave; its lateral margin simple, lacking a marginal furrow. Posterior angle of 1st epimeron sharply rounded and not cleft. On ventral surface of epimeron is a small rounded lobe which has no connection with lateral margin (see Fig. 175). Surface anterior to lobe not grooved or ridged. Posterior angle of 2nd epimeron rounded and not cleft. On ventral surface of 2nd epimeron is a small bluntly rounded lobe, situated well in front of posterior angle, and not connected with epimeral margin (see Fig. 175). Ventral surface of 3rd epimeron slightly thickened near its anterior margin. Epimera of 3rd and 4th segments trapezoidal and rounded posteriorly; those of 5th–7th segments quadrangular, with posterior angles almost right-angled on 5th and 6th and subacute on 7th. Epimera of all segments directed backwards. Between epimera, posterior borders of all tergites run straight. Ratio of length of pronotum to length of entire tergite (measured in the mid-line) 1 : 4·2 in 2nd segment and approximately 1 : 3·6 in 3rd–7th segments. Lengths in 2nd segment: pronotum 0·33 mm, entire tergite 1·40 mm; lengths in 3rd segment: pronotum 0·41 mm, entire tergite 1·50 mm. There is a shallow, median, semicircular groove on 1st tergite, otherwise dorsal surface of pereion almost smooth, tergites being only slightly rugose on each side above bases of epimera. Tergites have covering of rounded scales and also bear scattered scale-setae. Scale-seta (Fig. 176) has a short broad scale portion produced posteriorly in centre to form a club-shaped fold into which a short seta projects.

Pereiopods.—First leg has numerous spines set close together to form a brush on under surface of meros and carpos; otherwise as described for *C. hickmani*. Spines on under surface of meros become progressively sparser on 2nd–7th legs.

Male organ.—As described for *C. hickmani*.

Pleon.—Outline of pleon semicircular, continuous with that of pereion. Pleura of 3rd–5th segments expanded laterally, and curved backwards, sub-rectangular in shape with 4th and 5th pairs each successively narrower than preceding pair. First to 5th segments smooth dorsally; betwen pleura their posterior borders evenly curved. No lobes on ventral surface of 3rd–5th pleura. Terminal segment (Fig. 177) curves inwards on both sides at about middle of its length. Beyond this central narrowing, breadth of segment increases again slightly. Breadth across central constriction 0·70 mm; maximum breadth of posterior part 0·78 mm. Posterior border of segment straight. Dorsal surface of terminal segment raised into a broad, median, longitudinal ridge, which does not extend to posterior border. Tergites of pleon bear scales and scale-setae similar to those on pereion.

First pleopod (Fig. 178).—Exopodite subtriangular with apex bluntly rounded; a few spines on its ventral surface near apex. Tracheal part occupies outer half of exopodite. Endopodite styliform; its distal half curved outwards with a narrow chitinous thickening down outer border. A ridge, ornamented with spines and scales, extends down middle of dorsal surface of distal half of endopodite. Surface to inner side of ridge indented, forming a shallow groove. Near apex is a shorter ridge on each side of central ridge. There is a row of spinules on dorsal surface near inner border of endopodite.

Second pleopod.—Exopodite as described for *C. hickmani*. Length of articles of endopodite: 1st 0·33 mm, 2nd 1·32 mm. Length of flagelliform portion of 2nd article 0·46 mm. Otherwise endopodite as described for *C. hickmani*.

Third pleopod.—As described for *C. hickmani*.

Uropod (Figs. 177, 179).—Basal surface of protopodite oblique, visible in dorsal view of uropod; it occupies approximately one-third length of entire protopodite; its breadth less than length of protopodite. Length of basal surface 0·31 mm; breadth of basal surface 0·65 mm; length of entire protopodite 0·90 mm. Beyond basal surface, inner border of protopodite very shallowly incurved so that free lobe of protopodite gradually becomes narrower posteriorly; its posterior margin obliquely truncate with corners bluntly rounded. Greatest length of lobe 0·70 mm; length of posterior margin 0·25 mm. Area of protopodite visible to outer side of terminal segment, when uropod is attached, longer on its inner side than it is broad; length (along inner edge as far as indentation of terminal segment) 0·53 mm; breadth (in a line across insertion of exopodite) 0·38 mm. Exopodite subconical and very short, inserted on dorsal surface of protopodite, away from its inner border. Anterior to insertion of exopodite, surface of protopodite is raised into a subtriangular prominence. When uropod is attached, inner angle of prominence overlaps lateral border of terminal segment. Endopodite inserted on ventral surface, near inner border, at base of protopodite. It is subcylindrical, broadening distally, with apex very bluntly rounded. Endopodite terminates far in front of posterior border of terminal segment. Length of rami: exopodite 0·09 mm, endopodite 0·35 mm.

Female

Length of largest specimen 8·4 mm, breadth 4·2 mm. Female differs from male in the following structures:

Pereiopods.—Spines on under surface of meros and carpos less numerous than on corresponding legs of male.

First pleopod (Fig. 180).—Exopodite subrectangular, very short and broad; inner laminar part and outer tracheal part subequal in area. Endopodite not developed.

Second pleopod.—Exopodite as described for *C. hickmani*. A conical process, projecting back from inner side of protopodite, probably represents an endopodite.

Third pleopod.—As described for *C. hickmani*.

Habitat

Type locality.—Description is based on specimens found enrolled and buried in moist sandy soil at the base of a cliff above the shore at Roaring Beach, South Arm, on 8.iii.1957; 74 males and 63 females obtained.

Other localities.—Specimens were found in debris on ledges of a cliff above the shore at Tinderbox.

Variations

In small specimens, lateral processes of clypeus are relatively shorter and blunter than those of mature specimens; however, cephalon of the former is still

distinct due to transverse groove on frons. The slight rugosity on sides of pereial tergites is a little more pronounced on smaller specimens.

Cubaris tamarensis, sp. nov.

Figs. 181–192

Location of type specimens.—Holotype male and allotype female in the Australian Museum, Sydney. Paratype male and female in the Western Australian Museum, Perth. Paratype male and female in the Department of Zoology, University of Tasmania, Hobart.

Male

Size.—Length of largest specimen 10·0 mm, breadth 4·5 mm.

Colour.—Background colour of dorsal surface in live animal dark grey. Cephalon and pereion exhibit unpigmented patches. Protopodites of uropods orange-brown at base, shading to dark grey at posterior end.

Cephalon (Fig. 181).—Surface of vertex slightly uneven but not tuberculate. Frontal line forms an uninterrupted curved ridge, bent back towards vertex. Surface of frons has a shallow depression on each side to receive 2nd antennae. Above these depressions frons is pressed backwards. No deep groove across surface of frons. Lateral lobes of clypeus appear right-angled in anterior view and are scarcely produced upwards. Eyes rounded, each composed of 15 ocelli.

First antenna.—As described for *C. hickmani.*

Second antenna.—Length of peduncle 3·00 mm; length of articles of flagellum: 1st 0·17 mm, 2nd 0·55 mm. Setae as described for *C. hickmani.*

Left mandible (Fig. 182).—Incisor process consists of 1 strongly bifid tooth and 1 simple tooth. There are 2 pencils of setae on setose lobe and 2 pencils behind lobe.

Right mandible (Fig. 183).—One pencil of setae on setose lobe and 3 pencils behind lobe. Otherwise mandibles as described for *C. hickmani.*

First maxilla.—Outer lobe as described for *C. hickmani.* Inner lobe (Fig. 184) bears 2 rather short, thick, blunt setose processes.

Second maxilla.—On dorsal surface at base of inner lobe is a V-shaped band of chitin. No coarse setae in notch between lobes. Otherwise as described for *C. hickmani.*

Maxilliped (Fig. 185).—Distal set of setae on inner border of endopodite consists of 1 large seta and 4 smaller setae. Otherwise endopodite as described for *C. hickmani.* Endite subquadrangular with outer apical angle rounded. On its ventral surface near apex are 3 large spines which decrease in length from innermost one outwards. A short blunt spine is set in a depression at inner apical angle.

Pereion.—First epimera acute anteriorly. Outer side of 1st epimeron revolute so that dorsal surface of epimeron is concave. Actual lateral border of epimeron moderately sharp. Posterior angle of 1st epimeron rounded, its borders entire, not interrupted by a cleft. On ventral surface of epimeron (Fig. 186) is a sharply

rounded lobe which terminates a little in front of posterior border and results in formation of a moderately deep fissure on under side of epimeron. Sharp outer

Figs. 181–192.—*Cubaris tamarensis*, sp. nov.: *181*, cephalon, anterior view (antennae and mouthparts removed); *182*, distal part of left mandible, dorsal view; *183*, distal part of right mandible, dorsal view; *184*, distal part of inner lobe of right 1st maxilla, ventral view; *185*, distal part of left maxilliped, ventral view; *186*, right epimera of 1st and 2nd segments of pereion, ventrolateral view; *187*, scale-seta on dorsal surface of 1st segment of pereion, dorsal view; *188*, terminal segment and uropods, dorsal view; *189*, left 1st pleopod of male, dorsal view; *190*, right uropod, dorsal view; *191*, right 1st pleopod of female, ventral view; *192*, right 2nd pleopod of female, ventral view.

edge of this lobe is continuous with a low ridge which extends forwards on under surface of epimeron and gradually becomes obliterated in anterior third of segment.

Ridge is not connected with outer border of epimeron. Second epimeron trapezoidal; its posterior angle rounded. On ventral surface of 2nd epimeron (Fig. 186), well in front of posterior angle, is an oblique, sharply rounded lobe which results in formation of a moderately deep fissure on under side of epimeron. Anterior edge of lobe is connected with anterior border of epimeron by a ridge. Lobe does not project beyond borders of epimeron. Under surface of 3rd epimeron slightly thickened near its anterior border. Third and 4th epimera trapezoidal and rounded posteriorly. Fifth to 7th epimera quadrangular with posterior angles forming rounded right angles. Epimera of all segments directed backwards. Between epimera, posterior borders of all tergites run straight. Ratio of length of pronotum to length of entire tergite (measured in the mid-line) 1 : 4·1 in 2nd segment and approximately 1 : 3·7 in 3rd–7th segments. Lengths in 2nd segment: pronotum 0·38 mm, entire tergite 1·58 mm; lengths in 3rd segment: pronotum 0·44 mm, entire tergite 1·65 mm. There is a very shallow, median, semicircular groove in anterior half of 1st tergite, and on all tergites there is a slightly rugose area on each side above bases of epimera; remainder of dorsal surface of pereion smooth. Tergites have covering of rounded scales and also bear numerous scattered scale-setae. Scale-seta (Fig. 187) has a broad basal scale part which is curved backwards on each side and joined in middle to a long sheath, pointed at apex; a seta projects into base of sheath.

Pereiopods.—First leg has numerous spines set close together to form a brush on under surface of meros and carpos; otherwise as described for *C. hickmani*. Spines on under surface of meros and carpos become progressively sparser on 2nd–7th legs.

Male organ.—As described for *C. hickmani*.

Pleon.—Outline of pleon semicircular, continuous with that of pereion. Pleura of 3rd–5th segments expanded laterally and curved backwards, sub-rectangular in shape with 4th and 5th pairs each narrower than preceding pair. Posterior borders of 1st and 2nd segments evenly curved; between pleura, those of 3rd–5th segments run straight. Dorsal surface of 1st–5th segments smooth. No lobes on ventral surface of 3rd–5th pleura. Terminal segment (Fig. 188) curves inwards on both sides at about middle of its length; beyond this narrowing its breadth increases again considerably. Breadth across central constriction 0·90 mm; maximum breadth of posterior part 1·12 mm. Posterior border straight. Dorsal surface of basal part of terminal segment slightly raised into a broad, median eminence. Tergites of pleon bear scales and scale-setae like those on pereion.

First pleopod (Fig. 189).—Exopodite subtriangular with apex bluntly rounded and outer border incurved. It is divided into inner laminar part and somewhat smaller, outer tracheal part. Spines on ventral surface of apical angle. Endopodite styliform, its distal half curved outwards with a narrow chitinous thickening down outer edge. On dorsal surface a ridge, ornamented with scales, extends down centre of distal part of endopodite. Surface to inner side of ridge indented, forming a shallow groove. There is a shorter less-prominent ridge to outer side of central ridge. A row of spinules present on dorsal surface near inner border of endopodite.

Second pleopod.—Exopodite as described for *C. hickmani*. Length of articles of endopodite: 1st 0·52 mm, 2nd 1·52 mm. Length of flagelliform portion of 2nd article 0·54 mm. Otherwise endopodite as described for *C. hickmani*.

Third pleopod.—As described for *C. hickmani*.

Uropod (Figs. 188, 190).—Basal surface of protopodite oblique, visible in dorsal view of uropod; it occupies approximately one-third length of entire protopodite; its breadth less than length of protopodite. Length of basal surface 0·31 mm; breadth of basal surface 0·65 mm; length of entire protopodite 0·85 mm. Beyond basal surface, inner border shallowly incurved so that free lobe of protopodite gradually becomes narrower posteriorly; its posterior margin straight, slightly oblique, with corners bluntly rounded. Greatest length of lobe 0·62 mm; length of posterior margin 0·21 mm. Area of protopodite visible to outer side of terminal segment, when uropod is attached, longer on its inner side than it is broad; length (along inner edge as far as indentation of terminal segment) 0·57 mm; breadth (in a line across insertion of exopodite) 0·40 mm. Exopodite very short and subconical, inserted on dorsal surface of protopodite away from its inner border. Anterior to insertion of exopodite, surface of protopodite is raised into a subtriangular prominence. When uropod is attached, inner angle of prominence overlaps lateral border of terminal segment. Endopodite inserted on ventral surface, near inner border, at base of protopodite. It is subcylindrical, slightly narrowing posteriorly, with apex moderately sharply rounded. It terminates distinctly in front of posterior border of terminal segment. Length of rami: exopodite 0·11 mm; endopodite 0·38 mm.

Female

Length of largest specimen 11·5 mm, breadth 5·0 mm. Female differs from male in the following structures:

Pereiopods.—Spines on under surface of meros and carpos less numerous than on corresponding legs of male.

First pleopod (Fig. 191).—Exopodite subrectangular, very short and broad; inner laminar part almost as large as outer tracheal part. Endopodite not developed.

Second pleopod (Fig. 192).—Exopodite subtriangular, very short and broad, with outer border incurved and apex rather bluntly rounded and not markedly elongated. Tracheal part occupies outer angle. A conical process, projecting back from inner side of protopodite, probably represents an endopodite.

Third pleopod.—As described for *C. hickmani*.

Habitat

Type locality.—Description is based on specimens found in debris under grass tussocks growing immediately inland from the shore of the Tamar R. at Swan Point, West Tamar, on 27.xii.1957; 7 males and 21 females obtained.

Other localities.—Specimens were found under stones and debris on the ground immediately inland from a beach at West Ulverstone.

Variation

In one specimen outer lobe of left 1st maxilla has only 5 inner teeth, whilst that of right 1st maxilla has 7 inner teeth.

Genus SPHAERILLO Verhoeff

Sphaerillo Verhoeff, 1926, p. 295, non *Spherillo* Dana, 1852.
Chelomadillo Herold, 1931, p. 348.
Dryadillo Herold, 1931, p. 334.
Riudillo Verhoeff, 1937, p. 419.
Spherillo, section XIII, Budde-Lund, 1904, p. 87 (in part).

Type species *Sphaerillo pygmaeus* Verhoeff, 1926.

Dana (1852, p. 301, 1853, pp. 715, 719) gave very brief definitions of his genus *Spherillo.* In 1853 he described four new species, *Sph. monolinus, Sph. vitiensis, Sph. hawaiensis,* and *Sph. spinosus,* but did not designate any one of them as the type. He later (1854) established another species, *Sph. affinis.*

Budde-Lund (1904) extended the limits of *Spherillo* to include 65 species, grouping these into 13 sections and nominating a type for each section. He transferred *Sph. affinis* to his section II of *Armadillo,* but retained all four of Dana's original species in *Spherillo.*

Verhoeff (1926, p. 250) considered *Spherillo,* as it was treated by Budde-Lund, to be an unnatural genus. He preferred to spell the name as *Sphaerillo.* In keys to genera of Armadillidae Verhoeff restricted *Spherillo,* and (p. 295) named the restricted genus as "*Sphaerillo* (Dana) s.str.", but none of Dana's original species of *Spherillo* belong in *Sphaerillo* as limited by Verhoeff.

Jackson (1941, p. 2) believed Verhoeff's *Sphaerillo* to contain the species placed by Budde-Lund in his section XIII of *Spherillo* (this section did not include any of Dana's species). He noted that, according to Article 35 of the International Rules of Zoological Nomenclature, *Sphaerillo* Verhoeff is a homonym of *Spherillo* Dana, but (p. 3) expressed the opinion that workers on *Spherillo* had so consistently neglected to apply the International Rules of Nomenclature that it was too late to do more than protest formally, and, in the interest of clarity, to accept the situation. He suggested that *Sphaerillo* Verhoeff should therefore be retained as the generic name for the forms included under Budde-Lund's section XIII, and that *Spherillo* should be allowed to die out as its species became absorbed into new or existing genera. In addition to Verhoeff's species and those in section XIII, Jackson (p. 19) placed in *Sphaerillo* the following: *Sphaerillo* (*Xestodillo*) *marquesarum* (Jackson, 1933) and *Sphaerillo societatus* (Maccagno, 1932).

One of the species in Budde-Lund's section XIII, *Spherillo misellus* (Budde-Lund, 1885) Budde-Lund, 1904, was recorded from Tasmania by its author. If Jackson's proposal is followed, this species should be placed in *Sphaerillo.* However, as Verhoeff altered his concept of *Sphaerillo* in different papers, mostly without explaining his reasons for doing so, I have attempted to clarify the position of the genus before accepting Jackson's assignment to it of section XIII

of *Spherillo*, and consequently of *Sph. misellus*. The following account of Verhoeff's work on *Sphaerillo* explains the situation.

Summary of Previous Work on Sphaerillo

Verhoeff (1926, p. 254) in his key *a*, section M, claimed that in *Sphaerillo*, if a groove continues forwards from the cleft in the posterior angle of the 1st epimeron, it does not extend to the anterior angle of the epimeron. In this paper he placed no restriction on the backward extent of the inner lobe of the 1st epimeron in relation to the outer posterior angle, the connection of the lobe on the 2nd epimeron with the epimeral border, or the presence of lobes on the under surface of the 7th epimera and the pleura. Verhoeff divided genus *Sphaerillo* into two new subgenera, *Sphaerillo* and *Xestodillo*, placing in subgenus *Sphaerillo* three new species, *Sph. pygmaeus*, *Sph. hebridarum*, and *Sph. fissus*, and assigning to *Xestodillo*, *Sph. zebricolor* (Stebbing, 1900) and two new species, *Sph. lifouensis* and *Sph. politus*. Verhoeff (pp. 258, 296, 301) referred to a species by the name of "*vittatus*", but no species was described under this name. However, the following statement on p. 357: "*Cubaris zebricolor* Stebb. = *Sphaerillo vittatus* Verh. in Litt.", shows that references to "*vittatus*" should be applied to *Sph. zebricolor*. Verhoeff (p. 303) stated that in *Sph. politus* the groove from the cleft in the 1st epimeron extends forwards to the anterior angle of the epimeron. This contradicts the limit for *Sphaerillo* set in his key *a*.

Verhoeff (1928, p. 209) established another new species, *Sph.* (*Sph.*) *opacus*.

Herold (1931, p. 321) transferred *Sph. hebridarum* to his new genus *Lobodillo*, as this species possesses characteristic lobes on the pleura. In the same paper he erected another two new genera, *Dryadillo* and *Chelomadillo*, stating (pp. 316, 335) that in *Dryadillo* the inner lobe of the 1st epimeron is short and does not reach the posterior angle of the epimeron, whereas in *Chelomadillo* (see pp. 316, 349) the inner lobe of the 1st epimeron is long, reaching about to the posterior angle; also (p. 349) that the cleft in the 1st epimeron in *Chelomadillo* is continuous with a groove which reaches to the anterior angle of the epimeron.

Verhoeff (1937) established a new genus, *Riudillo*, for one new species, *R. takakuwai*. In his remarks on the genus he (p. 419) claimed that the inner lobe of the 1st epimeron does not form a continuation of the epimeral border, but in his description of *R. takakuwai* (p. 420) stated that the inner lobe passes over into the lateral border of the epimeron, and his illustration (fig. 14) of this structure shows the inner lobe continuous with the lateral border. The inner lobe of the 1st epimeron in *R. takakuwai* terminates considerably in front of the posterior angle.

Verhoeff (1938, p. 3) considered that *L. hebridarum* had been wrongly placed in *Lobodillo* and transferred it to a new genus, *Melanesillo*. In a key to genera, he (p. 7, section *b*) stipulated the absence of lobes ("Phylacomeren") from the under side of the 7th epimera and the 3rd–5th pleura in *Sphaerillo*. In section *c* of this key *Sphaerillo* was further limited to forms in which the inner lobe of the 1st epimeron reaches, or projects beyond, the posterior border of the epimeron, and the inner lobe on the 2nd epimeron is connected with the epimeral

border. He referred to the genus as "*Sphaerillo* Verh. (= *Chelomadillo* Herold)", and on p. 6 claimed that *Chelomadillo* agrees with *Sphaerillo* in having the inner lobe of the 1st epimeron long, reaching to the posterior border, and that in these two genera the cleft in the epimeron continues as a groove which reaches about to the middle of the lateral border of the epimeron. But Herold (1931, p. 349) had stated that this groove in *Chelomadillo* extends to the anterior angle of the epimeron. In this (1938) key Verhoeff regarded *Dryadillo* as a separate genus, distinct from *Sphaerillo*.

Verhoeff (1942*a*, p. 96) described a species named "*Sphaerillo* (*Sphaerillo*) *montivagus* n.sp.". Evidently this is not the same as *Sphaerillo montivagus* (Budde-Lund, 1885) Jackson, 1941. A comparison of the characters of Verhoeff's species with those of Budde-Lund's species, as described by Budde-Lund (1885, p. 35), confirms that the two are distinct.

Verhoeff (1942*b*, p. 165) then interpreted *Chelomadillo, Dryadillo,* and *Riudillo* as subgenera of *Sphaerillo*. In a key to the subgenera he referred to *Sphaerillo* as "sub-genus *Sphaerillo* Verh. (= *Dryadillo* Her.)", and classed *Chelomadillo* as a subgenus distinct from subgenus *Sphaerillo*. Verhoeff claimed that the inner lobe of the 1st epimeron remains far in front of the posterior border of the epimeron in the subgenera *Sphaerillo* and *Riudillo*, whilst it almost or exactly reaches, or even extends beyond, the posterior border in *Chelomadillo* and *Xestodillo*. He distinguished *Riudillo* from subgenus *Sphaerillo* as the outer border of the 1st epimeron in *Riudillo* is thickened whereas in *Sphaerillo* it is narrow and sharp-edged. According to Verhoeff (1942*b*, p. 168), subgenus *Sphaerillo* then included, in addition to Herold's (1931) nine species of *Dryadillo*, the following: *Sph. pygmaeus, Sph. fissus, Sph. opacus, Sph. montivagus* Verhoeff, and a new species, *Sph. insularum*. But according to his original descriptions of the species, the inner lobe of the 1st epimeron in *Sph. pygmaeus* and *Sph. opacus* projects backwards as far as the posterior angle of the epimeron (at least when it is viewed from the outer side of the epimeron). These species therefore do not comply with the limits of subgenus *Sphaerillo* which Verhoeff set down on p. 165 of this same paper. *Sph. montivagus* Verhoeff and *Sph. insularum* both conflict with Verhoeff's (1938) limit on the lobe of the 2nd epimeron in having this lobe completely separated from the epimeral border.

It is apparent from this account of *Sphaerillo* that Verhoeff has caused a great deal of confusion regarding the limits and synonymy of the genus. He (1926) misinterpreted the relationship of his *Sphaerillo* with *Spherillo* Dana. In 1926 he restricted the extent of the groove continuous with the cleft in the 1st epimeron for the genus as a whole; then, in the same paper, included in the genus a species which belongs outside this restriction. He (1938) later synonymized with *Sphaerillo* a genus which likewise falls outside this restriction. His limit on the backward extent of the inner lobe of the 1st epimeron in relation to the posterior angle, as set down for genus *Sphaerillo* in 1938, is in direct opposition to that set down for the typical subgenus *Sphaerillo* in his 1942*b* paper; the same applies to the synonymy or distinction of *Chelomadillo* and *Dryadillo* which is dependant on this character. He also retained in subgenus *Sphaerillo* two species which conflict

with its limits as defined in that paper. Having restricted the character of the lobe on the 2nd epimeron in 1938 he subsequently placed in *Sphaerillo* two species which do not comply with this restriction. Probably this complicated situation partly results from the fact that a satisfactory type species has not been designated for genus *Sphaerillo*.

Type Species

Verhoeff (1926) naturally did not nominate one of his species as the type of *Sphaerillo* as he did not regard the genus to be new. Jackson (1941, p. 2) considered that if a type was to be sought for section XIII of *Spherillo*, it appeared that *Spherillo danae* Heller, 1868, must be nominated; he (p. 19) later named *Sph. danae* as the type species of *Sphaerillo*. This procedure was contrary to Article 30 of the Rules of Zoological Nomenclature. Budde-Lund (1904, p. 53) designated *Sph. montivagus* (Budde-Lund) as the type of his section XIII, and such designation should not be subject to change (see Section I (*a*) in Schenk and McMasters 1936, p. 34). *Sph. danae* was not referred to *Sphaerillo* by Verhoeff (1926), i.e. it was not included under the generic name at the time of its original publication, and should therefore be excluded from consideration as the type of this genus (see Section II (*e*) α in Schenk and McMasters (loc. cit.)). Therefore Jackson's designation of *Sph. danae* as the type of *Sphaerillo* should not be sustained. *Sph. montivagus* (Budde-Lund) cannot be regarded as the type of *Sphaerillo* for the same reason. Thus the genus to date has no satisfactory type species.

Of the six species placed in genus *Sphaerillo* by Verhoeff (1926), three belong in subgenus *Xestodillo*, *Sph. hebridarum* has been placed in another genus, and *Sph. fissus* is not typical as it possesses uropods of a kind characteristic of *Armadillo*, s.s., rather than of *Sphaerillo* (see Verhoeff 1926, p. 258). The remaining species, *Sph. pygmaeus*, which also has page precedence over the others, is thus the obvious choice for a type. I therefore designate *Sphaerillo pygmaeus* Verhoeff, 1926, as the type species of genus *Sphaerillo* Verhoeff, 1926.

Verhoeff (1926, p. 296) stated that the inner lobe of the 1st epimeron in *Sph. pygmaeus* projects backwards as far as the posterior angle of the epimeron. Thus this character in the type species complies with Verhoeff's (1938) restriction on the inner lobe of the 1st epimeron for genus *Sphaerillo* and contradicts his (1942*b*) later characterization of subgenus *Sphaerillo*. Even if Verhoeff's (1938) restriction for the whole genus is rejected, if subgenera are to be distinguished on this feature, the typical subgenus *Sphaerillo* must be characterized by the condition exhibited by the type species, and should therefore include only those species in which the inner lobe of the 1st epimeron projects backwards approximately as far as, or further than, the posterior angle. Thus Verhoeff's (1942*b*) synonymy of *Dryadillo* with subgenus *Sphaerillo* cannot be upheld. Also Verhoeff's figures (1942*a*, fig. 19, 1942*b*, fig. 1) of the 1st epimeron in *Sph. montivagus* Verhoeff and *Sph. insularum* both show the inner lobe terminating far in front of the posterior angle. These species can no longer be included in subgenus *Sphaerillo*.

The question now is whether it is preferable to accept Verhoeff's (1938) restriction on the inner lobe of the 1st epimeron and to reinstate *Dryadillo* and

Riudillo to their original rank of genera distinct from *Sphaerillo*, or to formally remove this restriction so that the species having the inner lobe terminating considerably in front of the posterior angle, which were included in *Sphaerillo* by Verhoeff (1942*b*), need not be removed from the genus because of this character. Verhoeff (1928, p. 209), in listing characters common to *Sph. pygmaeus* and *Sph. opacus*, noted that the inner lobe of the 1st epimeron in these species does indeed project backwards as far as the posterior angle when the epimeron is viewed from the outer side, but added that when it is seen from the inner side the inner lobe terminates a little in front of this angle. He illustrated the inner view in his figure 8 of *Sph. opacus*. Certainly the distance by which the inner lobe falls short of the posterior angle, as shown in this figure, is not considerable; unlike the condition shown in Herold's figure (1931, fig. 85) of the 1st epimeron in *Dryadillo hebereri*, which (p. 345) was noted as being characteristic of *Dryadillo*. Thus the distinction between subgenus *Sphaerillo* and *Dryadillo* remains. However, in view of this later qualification of Verhoeff's original description of *Sph. pygmaeus*, I prefer not to accept the (1938) restriction of the genus on this character of the 1st epimeron.

With regard to the other characters in doubt, the original description of *Sph. pygmaeus* is not of any assistance, as their condition in this species was not noted. However, Verhoeff (1928, p. 209) stated that *Sph. pygmaeus* is very closely related to *Sph. opacus*, yet in a comparison of the two species he did not mention the extent of the groove continuous with the cleft in the 1st epimeron, or the connection or otherwise of the lobe on the 2nd epimeron with the epimeral border. It therefore seems reasonable to assume that *Sph. pygmaeus* resembles *Sph. opacus* in these characters. According to Verhoeff's (1928, figs. 8, 9) drawings of *Sph. opacus*, this groove in the 1st epimeron terminates a considerable distance behind the anterior angle of the epimeron, and the lobe on the 2nd epimeron is connected with the epimeral border. This supports Verhoeff's (1926) restriction on the former character and his (1938) restriction on the latter. However, I am not convinced that it is advisable to confine *Sphaerillo* to these narrower limits. With the discrepancy regarding the typical state of the inner lobe of the 1st epimeron settled, the chief cause of confusion is removed, and it would cause fewer complications in the position of individual species to employ the wider limits on these two characters as well.

I therefore recognize the limits of genus *Sphaerillo* given by Verhoeff (1926, p. 252, 1938, p. 7) with the exceptions that the groove continuing forwards from the cleft in the 1st epimeron may extend to the anterior angle of the epimeron, the inner lobe of the 1st epimeron may terminate considerably in front of the posterior angle of the epimeron, and the lobe on the 2nd epimeron may be separated from the epimeral border. This allows species originally placed in *Dryadillo*, *Chelomadillo*, and *Riudillo* to remain in *Sphaerillo*.

In his (1938) key, Verhoeff used his restriction on the lobe of the 2nd epimeron in *Sphaerillo* to distinguish this genus from *Microdillo* Verhoeff, 1933, in which this lobe is separated from the epimeral border. However, in an earlier paper he (1933, p. 98) noted other differences between *Microdillo* and *Sphaerillo*,

so that with the restriction on the 2nd epimeron in *Sphaerillo* removed the two genera are still distinct.

I propose the following diagnosis of genus *Sphaerillo* Verhoeff based on the information on the genus given by Verhoeff (1926, pp. 252, 263, 295; 1938, p. 7), but emended on the points discussed.

Generic Diagnosis

Dorsal surface of animal smooth, rugose, or tuberculate, but lacking spines. Second antennae slenderly built with their greater part projecting out from cephalon. First tergite of pereion does not exhibit a well-developed median eminence. Posterior borders of 2nd–4th pereial segments either not incurved or only slightly incurved on each side. Lateral border of 1st epimeron either narrow and sharp-edged or thickened underneath. Posterior angle of 1st epimeron exhibits a deep cleft resulting in formation of an inner lobe which is continuous with lateral epimeral border and visible from outer side of epimeron. Inner lobe may project backwards approximately as far as, or further than, posterior angle of epimeron, or may terminate considerably in front of posterior angle. If a groove continues forwards from cleft in posterior angle, it may extend to anterior angle of epimeron or may terminate before reaching this angle. Lobe on 2nd epimeron may be connected with, or separated from, epimeral border. No lobes ("Phylacomeren" of Verhoeff 1938) present on under surface of 7th epimera or 3rd–5th pleura. Dorsal surface of terminal segment not keeled. Posterior border of terminal segment not deeply incised in mid-line. Pleopods occupy considerably more than one-third breadth of pleon. Exopodites of all pleopods possess pseudotracheae. Breadth of protopodite of uropod, if greater than length of protopodite, is not more than 1·25 times the latter. Length of basal surface of protopodite not more than one-third length of entire protopodite. Inner border of protopodite incurved, but not angularly indented near insertion of exopodite. Outer side of protopodite not produced outwards to form a triangular lobe. Exopodite of uropod varies in length, but if it is very short (one-quarter or less than one-quarter breadth of lobe of protopodite), then free lobe of protopodite, measured on its inner border up as far as lateral indentation of terminal segment, is longer than it is broad across the middle. In the exceptional case, e.g. *Sph. fissus* Verhoeff, 1926, where exopodite is very short and free lobe of protopodite not longer than broad, lateral border of 1st epimeron is narrow and sharp-edged underneath (thus distinguishing the species from *Armadillo,* s.s.). Surface of protopodite not raised posterior to exopodite.

Comparison of Assigned Species with Generic Diagnosis

Due to previous differences in the limits of the genus it seems advisable to compare the characters of all species assigned to it with this diagnosis. The original descriptions of these species have been examined accordingly.

Verhoeff (1942*a*, p. 97) stated that the 5th pleuron in *Sph. montivagus* Verhoeff has a lobe on its under surface. This should exclude the species from

Sphaerillo. However, as Verhoeff's description is brief, an attempt to place the species elsewhere on this alone appears inadvisable.

Four of the species included by Budde-Lund (1904) in his section XIII of *Spherillo* — *Spherillo parvus* (Budde-Lund, 1885); *Sph. lentus, Sph. ingens, Sph. caligans*, all Budde-Lund, 1904 — exhibit lobes on the under surface of the 3rd–5th pleura (according to Budde-Lund 1908, p. 271, in the case of *Sph. parvus*). These species are therefore excluded from *Sphaerillo*: they may possibly belong in *Lobodillo* or *Melanesillo*. The terminal segment of *Sph. brevis* Budde-Lund, 1904, is slightly keeled on its dorsal surface. The exopodite of the uropod in *Sph. coecus* (Dollfus, 1898) is completely atrophied. The protopodite of the uropod in *Sph. brevicauda* (Dollfus, 1898) is very short and broad. Thus these species may be wrongly placed in *Sphaerillo*. The original description of *Sph. pictus* Heller, 1868, is very inadequate and makes no mention of characters of the 1st epimeron.

Wahrberg (1922, p. 233) considered two of his new species, *Spherillo tuberosus* and *Sph. telsogrossus*, as belonging in Budde-Lund's section XIII of *Spherillo*. *Sph. tuberosus* is excluded from *Sphaerillo* on the form of the uropods. Verhoeff (1926, p. 270) connected this species with his new genus *Acanthodillo*. According to Wahrberg (p. 249) an inner duplicature is represented as a thickening on the 5th–7th epimera in *Sph. telsogrossus*. As lobes are absent from the 7th epimera in *Sphaerillo*, the position of *Sph. telsogrossus* in this genus is doubtful.

As far as can be ascertained from the original descriptions, the characters of the remaining species assigned to *Sphaerillo*, including those of *Sph. misellus*, do not conflict with the diagnosis of the genus proposed in the present paper.

Where subgenera are concerned, I am not certain of the relationship of *Chelomadillo* with subgenus *Sphaerillo*. With the latter restricted to species having the inner lobe of the 1st epimeron projecting backwards as far as, or further than, the posterior angle, as I suggest, Herold's species of *Chelomadillo* agree with it in this regard. However Herold (1931) did not note whether the lateral border of the 1st epimeron in these species is narrow and sharp-edged as in subgenus *Sphaerillo*, or thickened as in *Xestodillo*. I therefore recognize the species originally placed in *Chelomadillo* as belonging in genus *Sphaerillo*, but do not classify them further into a subgenus.

Genus *Sphaerillo* Verhoeff, 1926, therefore appears to contain the following species:

(1) Species not included in Budde-Lund's section XIII of *Spherillo*: *Sphaerillo* (*Sphaerillo*) *pygmaeus* Verhoeff, 1926 (type species); *Sph.* (*Sph.*) *fissus* Verhoeff, 1926; *Sph.* (*Sph.*) *opacus* Verhoeff, 1928; *Sph.* (*Xestodillo*) *zebricolor* (Stebbing, 1900); *Sph.* (*X.*) *lifouensis, Sph.* (*X.*) *politus*, both Verhoeff, 1926; *Sph.* (*X.*) *marquesarum* (Jackson, 1933); *Sph.* (*Dryadillo*) *feuerborni, Sph.* (*Dr.*) *bedaliensis, Sph.* (*Dr.*) *baliensis, Sph.* (*Dr.*) *arcangelii, Sph.* (*Dr.*) *schellenbergii, Sph.* (*Dr.*) *montanus, Sph.* (*Dr.*) *hebereri, Sph.* (*Dr.*) *magnificus, Sph.* (*Dr.*) *sexlineatus*, all (Herold, 1931); *Sph.* (*Riudillo*) *takakuwai* (Verhoeff, 1937); *Sph.*

setosus, *Sph. tuberifrons*, *Sph. pustulosus*, *Sph. nitens*, all (Herold, 1931); *Sph. societatis* (Maccagno, 1932); *Sph. insularum* Verhoeff, 1942.

(2) Species included in Budde-Lund's section XIII of *Spherillo*: *Sph. danae* (Heller, 1868); *Sph. montivagus*, *Sph. misellus*, *Sph. obscurus*, all (Budde-Lund, 1885); *Sph. melanurus* (Dollfus, 1886); *Sph. floresianus*, *Sph. velutinus*, *Sph. weberi*, all (Dollfus, 1898); *Sph. setaceus*, *Sph. nobilis*, both (Budde-Lund, 1904).

The following species of section XIII of *Spherillo* may belong in *Sphaerillo*, but their descriptions give rise to some doubt regarding this: *Sph. ?pictus* (Heller, 1868); *Sph. ?coecus*, *Sph. ?brevicauda*, both (Dollfus, 1898); *Sph. ?brevis* (Budde-Lund, 1904); *Sph. ?telsogrossus* (Wahrberg, 1922).

Sph. montivagus Verhoeff appears to have been incorrectly placed in *Sphaerillo*, but an alternative position for this species cannot be suggested.

Sphaerillo misellus (Budde-Lund)

Armadillo misellus Budde-Lund, 1885, p. 285.
Spherillo misellus Budde-Lund, 1904, p. 93.
Sphaerillo misellus Jackson, 1941, p. 3 (implied).

Location of type specimen.—Berlin Museum.

The position of *Sph. misellus* in *Sphaerillo* is considered in the preceding discussion on the genus.

An English translation of Budde-Lund's (1885) description given by Thomson (1893, p. 72) contains some errors. Thomson translated "truncus utrinque manifesto tuberculatus" as "body everywhere distinctly tubercled". Budde-Lund's "truncus" obviously refers to the pereion as distinct from his "caudae" which refers to the pleon. This phrase should read: pereion distinctly tubercled on each side. Thomson translates "flagellum scapi articulo quinto brevius; flagelli articulus prior altero triplo vel magis brevior" as "flagellum 5-articulate, shorter than the peduncle; first articulation of the flagellum rather shorter than the next three". This should read: flagellum shorter than 5th article of peduncle; first article of flagellum three times or distinctly shorter than the other.

Budde-Lund (1885, 1904) recorded *Sph. misellus* from Tasmania. (In his 1885 paper Tasmania was called by its earlier name, Van Diemen's Land). Unfortunately he did not record the locality or conditions in which his specimen was found. I have not yet collected specimens which can be assigned to *Sph. misellus*.

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List of Genera and Species